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Optimising cattle genotypes and systems in Sub-Saharan Africa to increase productivity and reduce GHG emissions

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Declaration

I declare that this thesis is my own composition and that the research described in it is my own work, except where acknowledged. The work described has not been submitted for any other degree or professional qualification.

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Publications

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Abstract

Cattle are important in supporting development in Sub Saharan Africa (SSA) as they are a source of both food and income. However studies show there is a substantial gap between the potential and realised production levels, leading to potential profit and efficiency levels not being reached. In particular, herds that have poor efficiency also tend to produce more greenhouse gases (GHGs) per unit of food product. The lack of consistent recording systems for both pedigree and performance data makes traditional selective breeding to improve profitability and efficiency, difficult. Crossbreeding strategies require comparatively little data, are generally easy strategies to follow and results can be achieved more quickly, so are a good fit in SSA systems. Crossbreeding also allows farmers to take advantage of the complementary fitness traits from local breeds and production traits from exotics, as well as providing favourable heterosis. In order to determine an optimal crossbreeding strategy, models which predict the long-term outcomes of varying strategies are needed. Therefore, this thesis describes number of models which can be combined for this purpose.

Initially, a meta-analysis of heterosis in cattle in the tropics was carried out in order to characterise the expression of heterosis, which is an important factor in determining the performance of crossbreds and crossing strategies. In particular, the effect of trait, breed pair and climate were examined. In total, 62.5% of estimates were found to be significantly different from zero, the majority of which (89.8%) were beneficial for the studied trait. Milk, longevity and health traits were found to show the greatest heterosis, which showed great potential of crossbreds to increase performance for these traits which are strongly linked to profitability and efficiency. Crosses between more distantly related breeds showed moderate to high heterosis, whereas crosses between breeds of a similar type did not express heterosis that was significantly different from zero. These results show that

heterosis has significant and favourable impact on productivity of cattle farming in tropical production systems.

In order to model how herd composition changes over time, fertility parameters are needed for different crossbred individuals. In particular, age-specific calving rates, the probability a cow will calve at a given age, were needed. The results of the meta-analysis showed that the fertility traits more commonly recorded were age at first calving and calving interval. Therefore three variations of a model that used these as input parameters to predict age-specific calving rates were developed. These were tested using both input parameters for Ethiopia, but also from UK dairy cattle, where the predicted values could be compared to observed values. All three models performed well under both scenarios (R^2 from 0.98-1.00), with the model in which estimation errors were reduced by reducing the size of age class considered, performing the best.

Next, a deterministic herd model, which predicted the effect of crossing strategy on herd composition, using input parameters from the fertility model, was combined with a genetic model which used breed additive, heterosis and recombination effects from studies in the meta-analysis, to predict the performance of varying types of crossbred individuals for a given trait. This allowed for the prediction of herd performance for a given trait under varying crossbreeding strategies. These models were tested using a case study of Boran-Holstein crossbreeding in Ethiopia. Herd performance for annual milk yield and yearling weight was predicted under a range of crossing strategies. For milk yield, strategies which increased the proportion of Holstein genetics, whilst maximising heterosis and reducing recombination, tended to perform best. For yearling weight, all strategies increased the herd performance of this trait compared to the initial herd of purebred Borans, which is

undesirable as heavier yearlings have greater feed costs. Strategies that minimized the proportion of Holstein genetics, such as using a crossbred sire, tended to perform best.

In order to predict an overall optimal strategy for a given system, rather than considering traits individually, models which combined the results for multiple traits were needed to predict annual herd profit and GHG emissions. These models were developed using the International Panel on Climate Change (IPCC) guidelines for a tier II approach and input parameters specific to the Ethiopian case study were used where possible. For annual profit, crossbreeding strategies that maximised heterosis tended to perform best. In particular, a true rotation strategy, where sire breed was alternated every generation, allowed for heterosis to be maximised and so led to the greatest increase in annual profits. For GHG emissions, crossbreeding strategies that minimized the proportion of Holstein genetics tended to perform best, producing the fewest kilograms of carbon dioxide (CO_2) equivalents. In particular, a strategy where the herd were graded up to a maximum of 50% Holstein, using an first cross (F1) bull, consistently produced the least GHGs, compared to all but a herd of purebred Boran. However, in order to reduce GHGs whilst maintaining food production levels, emission intensities (kg CO_2 equivalents per unit of food produced), rather than gross emissions can be considered. Results showed that the true rotation strategy, which produce high levels of milk but not the highest gross GHG emissions perform best when the aim is to minimize GHGs per unit of milk produced.

Lay Summary

Cattle are important in supporting development in Sub Saharan Africa (SSA) as they are a source of both food and income. However studies show that farms tend not to be as productive as they could be and this means there is potential to increase their profit and reduce greenhouse gas emissions per unit of milk produced.

Although animal breeding is considered a good strategy to improve productivity, selective breeding where bulls are judged by the performance of their relatives, is difficult to achieve in SSA. This is mainly due to a lack of consistent recording. Crossbreeding strategies, where animals of different breeds are bred together, require comparatively little data, are generally easy strategies to follow and results can be achieved more quickly, so are a good fit in SSA systems. Crossbreeding also allows farmers to take advantage of both the robustness from local breeds and high milk production from exotic breeds. Crossbreds also express heterosis, which is a phenomenon where a crossbred tends to perform better than the average of its purebred ancestors.

In this thesis, models are developed to predict how a variety of types of crossbreeding would affect the milk production, profit and greenhouse gas emissions from a herd. These are then applied to a case study of a herd of Boran, a local zebu breed, which are crossed with Holsteins, a highly productive breed, originating from Europe. The results showed that although using a crossbred bull led to the smallest increases in greenhouse gas emissions per cow, a rotational strategy where the bull used was alternated between Boran and Holstein every generation, led to the greatest increases in milk, profit and greenhouse gas emissions per kg of milk. Therefore this strategy would be good for Ethiopian farmers to adopt.

List of Abbreviations

AFC	Age at first calving
AI	Artificial insemination
CI	Calving interval
CO_2	Carbon dioxide
DTR	Delayed true rotation strategy
E	Exotic breed, European *Bos taurus*
EI	Emission intensity
F1	First cross
FPCM	Fat and protein corrected milk
GHG	Greenhouse gases
IPCC	International Panel on Climate Change
$kgCO_2eq$	Kilograms of carbon dioxide equivalents
L	Local breed
LCA	Lifecycle Assessment
LSM	Least Square Mean
MAE	Mean absolute error
SSA	Sub-Saharan Africa
T	Tropical *Bos taurus*
TR	True rotation strategy
UTR	Unbalanced true rotation strategy
Z	*T*ropical *Bos indicus,* also known as zebu

List of Tables

List of Figures

Table of Contents

Chapter 1: General Introduction

1.1 Importance of cattle in sub-Saharan Africa

Livestock are important in supporting development in sub-Saharan Africa (SSA) as they are a source of both food and income. In terms of food security, livestock provide an important source of calories (Randolph et al., 2007), but more specifically protein and micronutrients. In particular, vitamins A and B_{12}, calcium, iron, riboflavin and zinc, which are especially important for children and mothers, are difficult to acquire from plant-only sources but are found in much higher densities in foods of animal origin (FAO, 2009). Livestock also help to stabilize food supply. The fluctuating production of crops can limit the availability of food for humans, but animal-sourced food, particularly milk and eggs, act as a buffer to these fluctuations, providing an important food source when crop availability is low (Wilson et al., 2005; FAO et al., 2010).

Livestock farming is also important for the financial security of many people, particularly the rural poor but also across income levels (Pica-Ciamarra et al., 2014), accounting for 27% of agricultural GDP in SSA (FAO et al., 2010). An increase or intensification in livestock farming is recommended as a good strategy for poverty reduction (FAO et al., 2010; Pica-Ciamarra et al., 2014), due to the large share of the rural poor that are already engaged in livestock farming and increased demand for animal products.

Large increases in demand for animal products are predicted in SSA; for example, increases of 170%, 137%, 113% and 107% are predicted from 2000 to 2030 for poultry, mutton, beef and milk respectively (Robinson and Pozzi, 2011). These increases will be primarily driven by a large increase in population in the region (Haub and Kaneda, 2013), but also increased urbanization, increases in income and a change in diet composition (FAO, 2017a). Cattle are

a particularly important species to meet this increased demand. Milk is the largest source of animal protein per unit of volume (Pica-Ciamarra et al., 2014) and dairy has been shown to be an area with particularly strong potential for growth (Wood et al., 2006), in part due to the large gaps between potential and realised production levels (Henderson et al., 2016). Increasing productivity of cattle farming to meet this increase in demand will support both food and financial security in SSA.

1.2 Productivity and profitability

1.2.1 Strategies to increase productivity and profitability

A simple strategy to increase production to meet this increased demand is to increase the number of animals. Results of surveys suggest this could also increase income, as across a range of African countries, business-oriented livestock farmers (those who receive at least 25% of income from livestock farming) tend to have twice as many animals as the average farmer (Pica-Ciamarra et al., 2014). However, unlike poultry and pig production systems, dairy farming tends to have fewer economies of scale due to higher labour requirements and so increases in herd size result in smaller increases in profit compared to other livestock species (FAO, 2009), despite increasing food production. Another factor is the increased environmental impact of an increased national herd size. Cattle farming has many negative environmental impacts, including overgrazing, reducing water availability, competing for human food, and greenhouse gas emissions (FAO, 2009). Therefore simply increasing the number of cattle is not desirable.

Instead, increasing productivity per cow is a good strategy to increase food and financial security. A substantial gap between the potential and realised production levels for livestock farming present in SSA is due to shortfalls in management, but also choice of appropriate

animal genotypes (Henderson et al., 2016). Access to and quality of feed is a major constraint for productivity. Ruminants across developing countries suffer from permanent or seasonal nutritional stress (FAO, 2003). Rather than relying solely on low quality roughages, increases in the use of concentrate feeds, e.g. for SSA from 15 million tonnes in 1980 to 47.6 million tonnes in 2005 (FAO, 2009), will increase animal production levels. However, access to these feeds is limited (Chakeredza et al., 2008) and production can compete with human food production (Mottet et al., 2017). Alternative feed sources, including use of fodder trees and legumes (Chakeredza et al., 2008) or by-products of the sugar, brewing or other food processing industries (Bediye et al., 2018) have been researched to mitigate the need for concentrates whilst still increasing feed quality.

Presence of diseases and low access to veterinary medicines also limit productivity. For example, in Tanzania, tick-borne diseases are estimated to cause a loss of 364 million USD per year (Kivaria, 2006). In particular in SSA, diseases including trypanosomiasis (Bauer et al., 1999; MacLeod et al., 2018), East Coast fever (Di Giulio et al., 2009), foot and mouth disease (Lyons et al., 2015), bovine tuberculosis (Vordermeier et al., 2012), and mastitis (Duguma et al., 2012) limit the productivity of cattle, either by reducing production per animal or by increasing death rates. Vaccinations and other veterinary interventions would mitigate these losses, but access to these are not always widespread (Di Giulio et al., 2009; Duguma et al., 2012). Some breeds of cattle are also known to be resistant or tolerant to these diseases (Vordermeier et al., 2012; Kim et al., 2017; Vajana et al., 2018). Increasing the use of resistant cattle would increase the productivity of cattle, either enhancing the performance of individuals, or by reducing deaths of cattle.

1.2.2 Selection to increase productivity and profitability

As well as reducing disease burden, selection for animal productivity is a good strategy to increase productivity and profitability of farms. Unlike management options, selection of animals is a more permanent solution that does not carry the same recurring costs. It also has the potential to be cumulative if selective breeding is carried out over subsequent years. For example, in the US, the average lactation milk yield of Holstein cattle has increased from about 6000 kg in 1960 to about 12,000 kg in 2000 and about half of this increase is thought to be due to selective breeding (Dekkers and Hospital, 2002). In Africa, milk yields tend to be much lower, with averages of 1,500 L per year in Kenya (Ojango et al., 2014). Despite widespread animal breeding programmes across temperate countries, sustainable breeding programmes are rarer in Africa due to lack of investment and infrastructure and the heterogeneity of systems (Marshall et al., 2019). Typically, animal breeders use quantitative genetics techniques which combine pedigree information and phenotype data to produce estimated breeding values which can be used to judge the genetic merit of an individual (Simm, 2000). However, these require both pedigree and phenotypic data which are not routinely collected in SSA; the variation in systems results in greater variation in phenotypes as well as variation in breeding goals.

1.3 Greenhouse gas emissions

1.3.1 Impact of Cattle Farming on GHG emissions

Whilst increasing productivity and profitability is important, the environmental impact of cattle should be also be considered. Globally, livestock farming makes a significant contribution to greenhouse gas (GHG) emissions, producing CO_2, methane and nitrous oxide, accounting for around 15-18% of the total GHG produced (FAO, 2013; Opio et al.,

2013). The majority of these emissions (64-78%) are due to cattle farming (Gerber et al., 2013; Herrero et al., 2013b). In developing countries these emissions are increasing. Between 1961 and 2010 the livestock emissions in developing countries, including those in SSA, increased by 117% (compared to a decrease of 23% in developed countries), largely due to an increase in methane emissions from beef and dairy cattle production (Caro et al., 2014).

As previously discussed, demand for animal products is predicted to increase in SSA. There is a need to increase productivity to meet this demand without increasing related GHG emissions. This can be achieved by decreasing the emission intensity, which is the amount of GHGs produced per unit of product. Emission intensity is usually expressed as CO_2 equivalents (a unit that expresses the amount of any GHG including methane and nitrogen dioxide as the functionally equivalent amount of CO_2, accounting for their varying global warming potential) per unit of product, or per unit of value (e.g. economic or dietary value, allowing comparisons between products).

Current emission intensities for livestock farming in SSA are some of the highest in the world. Eritrea, Niger and Ethiopia have the highest emission intensities, producing 75.6, 40.7 and 40.6 kgCO_2eq/$ respectively (Caro et al., 2014). Emission intensity can be calculated either by allocating emissions to only the main products (milk and meat) or to products as well as other uses (Opio et al., 2013). For SSA there is a large difference between the results of these methods as cattle are usually kept for a range of uses in addition to milk or meat, including draught power (Ouma et al., 2005; Mwacharo and Drucker, 2005), manure (Lekasi et al., 2001; Herrero et al., 2013a) or as a capital asset (Bebe et al., 2003a). However, even after allocating emissions to draught and manure, SSA has the highest emission intensity for milk, 9 kg CO_2eq/kg, compared to 1.6 CO_2eq/kg in Western

Europe (Opio et al., 2013). Herrero et al. (2013) suggest that this is driven by the low productivity in SSA and that there is good potential to reduce emission intensity through improved production and efficiency.

1.3.2 Strategies to reduce GHG emissions and emission intensities

A number of management options have been suggested to reduce GHG emissions in cattle farming. There is good evidence that a diet with increased concentrates can reduce GHG emissions (Johnson and Johnson, 1995; Doreau et al., 2011) as concentrates have a high digestibility and so cattle fed concentrates produce less methane and manure (Boadi et al., 2004; IPCC, 2006). However, the recurring costs to farmers means that increasing the amount of concentrates fed may not be widely feasible in SSA (Chagunda et al., 2015b). Alternatively, higher quality forage can be fed. In a Canadian study, beef cattle grazing alfalfa–grass pastures produced significantly less methane than those grazing grass only (McCaughey et al., 1999). Similarly, in a New Zealand study, dairy cattle produced less methane per unit of dry matter intake when grazing sulla, compared to rye grass (Woodward et al., 2002). Legumes such as sulla and alfalfa have a higher digestibility and increased rate of passage through the digestive system, leading to reduced enteric methane emissions (Johnson and Johnson, 1995). However in SSA there may be environmental issues with manipulating plant species in grassland. Chagunda et al. (2015b) also suggest that small land holding sizes may be a limiting factor. Many cattle in SSA are fed well below their intake limit (Chakeredza et al., 2008), meaning they are not reaching their potential productivity. Therefore simply increasing the overall food intake would be a good strategy to increase productivity and therefore reduce emission intensity. Other management options suggested include the manipulation of fermentation in the rumen by supplementing

diets with fatty acids (Mathison et al., 1998; Dohme et al., 2000; Dong et al., 2015), making the environment less hospitable for methanogenic archaea by reducing ruminal pH (Hegarty, 1999) and reducing the number of methanogenic archaea using chemical treatment (Henderson et al., 2018) or immunization (Subharat et al., 2015). However, as with all the management options, these solutions are not permanent and have recurring costs to the farmer.

1.3.3 Selection to reduce GHG emissions and emission intensities

Alongside any management options, farmers can select animals to reduce emission intensity. Unlike the management options, selection of animals is a more permanent solution that does not carry the same recurring costs. It also has the potential to be cumulative if selective breeding is carried out over multiple generations. Emission intensity can be reduced by selecting animals to reduce total emissions and increase total productivity. Total emissions are dependent on the emissions produced per animal and the number of animals needed.

There is some evidence for variation between animals in their enteric methane emissions. A study by Haque et al. (2015) measured methane emissions of dairy cows in two years. They found high variation within-cow compared to between-cow and repeatabilities were only 0.35-0.41. The diurnal variations were significant, with less methane produced at night, showing the importance of emission measurement over at least a full day. However, the correlation between methane emissions in years 1 and 2, once adjusted for energy-corrected milk, was fairly high (r=0.7). Other studies have estimated the heritability of enteric methane emissions, ranging from 0.12 to 0.45 in UK dairy cattle (Pickering et al., 2015; Breider et al., 2019), 0.21 in European dairy cattle (Lassen and Løvendahl, 2016) and

0.32 in Brazilian Nellore cattle (*Bos indicus*) (Sobrinho et al., 2015). In a study of beef cattle in the US, the heritability of methane production was estimated as 0.27. However, this was found to be highly genetically correlated with weaning weight (r=0.84±0.09), meaning that selection for reducing methane emissions could also result in a reduction of weaning weight, which is highly undesirable. The residual methane production (that is the difference between measured and expected production, predicted from dry matter intake) was found to be less heritable (h^2=0.19±0.06), but also less genetically correlated with weaning weight (r=0.32±0.22) (Donoghue et al., 2016). This means that selection on reduced residual methane production would not have the same negative effect on weaning weight.

Total emissions can also be reduced by breeding for characteristics that reduce the total number of animals needed. To avoid an adverse effect on total production, this is best achieved by reducing the number of replacement animals required. The total productive period of each animal can be increased by reducing age at first calving or by increasing longevity or lactation length and reducing unproductive periods. Wall et al. (2012) modelled the emission intensity of milk production in the UK with varying lactation lengths. Although the increased lactation lengths required fewer cows to produce the same level of milk, predicted GHG intensity rose due to reduced yields towards the end of long lactations. Fewer replacements will also be needed if fewer animals die or need to be culled. This could be achieved by selecting for health and survival traits, including disease resistance, drought tolerance and improved calving and maternal traits to reduce calf mortality (Wall et al., 2010). These fitness traits are likely to be increasingly important in SSA as climate change means the climate will become more extreme. Indeed, a simulation of disease control on GHG emissions in East Africa predicted that removal of trypanosomiasis resulted in a reduced emission intensity per unit of protein between 0-8% (MacLeod et al., 2018).

Emission intensity can also be reduced by increasing the productivity of animals without increasing GHG emissions. The can be achieved by selecting for reduced residual feed intake (RFI), which is the difference between the actual feed intake and the predicted feed intake for an animal at a given production level. Heritability estimates for RFI are moderate (0.2-0.4) (Khansefid et al., 2014) and it has been shown to be independent of production traits (Basarab et al., 2013). This means it is a good candidate trait for selection to reduce GHG intensity. However, its repeatability over time and across diets is moderate (r=0.33-0.67) (Basarab et al., 2013), showing that careful measurement over a long period is necessary for an accurate assessment.

Other studies predict that simply selecting for an increase in product yield leads to a decrease in GHG intensity (Wall et al., 2012). This is due to the large energy requirement of body maintenance (Mathison et al., 1998)). An increase in production per animal may lead to an increase in associated GHG emissions, but this is insignificant compared to the increase due to maintenance if additional animals are required (Chagunda et al., 2015b). For example, Kirchgessner et al. (1995) modelled European dairy cow GHG emissions and found that although an increase in annual production from 5000 to 10000 L would result in an increase of 23% in methane emissions per animal, methane emissions intensity would reduce by 40%. This can also been seen in real-world data. From 1988 to 1996, milk yield per cow in Queensland, Australia increased by 38% but methane emission intensity reduced by 26% (Howden and Reyenga, 1999). However, the potential increases in feed cost to meet these increases in yield must not be overlooked.

It is important to note that selection for most of these traits is to the benefit of the farmer. Reducing the number of animals and wastage (including costs of veterinary intervention) should reduce input costs. Increasing the productivity of cattle should increase profits.

In conclusion, breeding is a good strategy for both increasing productivity and profitability and reducing GHG emissions or emission intensity.

1.4 Breeding

1.4.1 Selective breeding in SSA

Selection can take place between individuals or between breeds and crossbreeds. Selection between individuals and continued selective breeding can allow permanent and cumulative gains. However, in SSA the majority of farmers are smallholders. Studies report low average herd sizes of e.g. 3.2 in the highlands of Kenya, (Bebe et al., 2003b), 5.9 in the Nakuru district, Kenya, 11.9 in the Western Province, Zambia (Moll et al., 2007), 3-16 in Nigeria and 5-6 in Ethiopia (Jabbar et al., 2002). These small herd sizes mean that selective breeding within herds is not realistic. In order to carry out selective breeding across herds a consistent recording system of both pedigree and performance data is needed, which is not widely found across SSA (Kahi et al., 2005; Mwacharo and Drucker, 2005; Chagunda et al., 2015a).

One solution to this is community based breeding programmes, where a group of farmers work together to improve their genetic resources (Mueller et al., 2015). In Ethiopia, community based sheep breeding programmes allow farmers to collaborate to carry out performance recording and selection of local rams according to their own selection criteria, specific to their local system (Haile et al., 2013). Results over a 10 year period showed 6 month weight, an economically important trait, increased between 0.11 and 0.21 kg per year across the different regions (Haile et al., 2020), which should lead to significant benefits for farmers. In Kenya, an NGO FARM Africa has also implemented community based breeding programmes to increase milk and meat production of local goats by crossbreeding

using exotic Toggenburg goats (Ojango et al., 2011). The project has led to large increases in profit for farmers, from 93 to 995 US dollars a year (Peacock, 2008). However, some unintended negative selection for growth rate has occurred, due to selling of fast growing bucks because of their large market value, rather than retaining them for breeding (Ojango et al., 2011). In a review of community based breeding projects, Mueller et al. (2015) note the lack of these projects for cattle. They suggest this may be due to smaller herd sizes and slower reproduction rate, as well as the success rate of artificial insemination (AI) in cattle compared to small ruminants (Mueller et al., 2015). The use of AI means that sires do not need to be kept locally, increasing the potential gene pool.

Community based selective breeding projects require significant infrastructure and cooperation. Selection between breeds or crossbreeding does not require data on this scale. Although cumulative gains are not possible in the same way, selection between breeds and crossbreeding can allow large and quick gains, particularly when current performance is low, without the same need for a recording system (Simm, 2000). Therefore in SSA where there is large potential to increase performance (Herrero et al., 2013b), as well as small herds (Jabbar et al., 2002) and a lack of systematic data collection (Chagunda et al., 2015a), selection between breeds or crossbreeding systems is, under current conditions, the more achievable and cost-effective option to increase productivity and reduce emission intensity of cattle farming.

1.4.2 Breeds and Crossbreeds in SSA

A large variety of breeds and crossbreeds of cattle are used in SSA. Improved temperate breeds (*Bos taurus*) are often imported to SSA (Chagunda et al., 2015b). These exotic breeds are often viewed favourably due to their high productivity. In a survey of farmers in

the Kenya highlands, 78% preferred exotic dairy breeds (Bebe et al., 2003a). The Malawi Canada Dairy Development Project allowed 400 Holstein-Friesian heifers to be imported from Canada to a farm in the south of Malawi to help support the desire for increased production (Chagunda et al., 2004). However, there are some problems with the use of exotic breeds. Although they are more productive, these exotic breeds were selectively bred under very different conditions and systems, making them less well adapted to conditions in SSA. The productivity of the Holstein-Friesian herd in Malawi dropped significantly over time, likely due to heat stress in the cattle (Chagunda et al., 2004).

There are also tropically-adapted local breeds. These can broadly be split into zebu (*Bos indicus*) and the tropical *Bos taurus*. They are much less productive than the exotic breeds, having undergone comparatively little artificial selection. However, originating from the tropics, they are well adapted to the environmental conditions. Indigenous breeds tend to have high heat and drought tolerance as they have survived many generations in arid conditions (Hammond et al., 1996; Ribeiro et al., 2009). They also tend to be more resistant to local diseases and parasites than their exotic counterparts (Mattioli et al., 2000). For example, trypanosomiasis, a disease carried by tsetse flies in parts of SSA, can have a devastating effect on cattle farmers, causing decreased production and eventual death of livestock. A number of West African taurine breeds have been shown to be resistant to the effects of the disease (Berthier et al., 2015).

1.4.3 Benefits of crossbreeding

Crossbreeding is a breeding strategy that allows farmers to take advantage of both the high production and high adaptation from exotic and local breeds, respectively, as well as beneficial non-additive genetic effects. In particular, heterosis, which in animal breeding is

usually defined as the difference between performance of a first cross (F1) and the mean performance of the two parental types, is often beneficial (Powers, 1944).

Breeders use crossbreeding to increase the overall performance of a wide range of species, particularly in plants (Crow, 1998; Duvick, 2001), but also for a range of different animal species, including sheep (Leymaster, 2002), pigs (Liu et al., 2004), poultry (Haberfeld et al., 1996) and beef cattle (Gregory et al., 1994). In dairy cattle breeding, the huge success in improving the Holstein breed for increased milk production has meant that purebred Holstein animals are widespread (reported in 162 countries (FAO DAD-IS, 2017)) and crossbreeding is less common in the dairy industry. However there is increased interest in crossbreeding (Sørensen et al., 2008), particularly in more extensive low-input systems, such as the pasture-based seasonal calving systems in New Zealand (Lopez-Villalobos et al., 2000; Buckley et al., 2014) as it allows the combination of the production traits from the Holstein and robustness traits from other dairy breeds.

Crossbreeding is also popular in the tropics (Cunningham and Syrstad, 1987; Rutledge, 2001) as improved temperate breeds with high production levels lack the robustness of local tropical breeds. Therefore, crossbreeding allows farmers to keep cattle with desirable traits from both exotic temperate and local tropical breeds. Also, exotic and local breeds tend to be distantly related and this is thought to increase the amount of heterosis which is usually beneficial (Powers, 1944).

1.4.4 Examples of crossbreeding programmes in SSA

Crossbreeding is widely used across SSA, but often without clear objectives or without following a systematic strategy. For example, in Kenya, most of the country's milk is produced by smallholder farmers who tend to keep crossbreds with mixed local and exotic

ancestry (Bebe et al., 2003a). However crossbreeding in these systems tends to be non-systematic and neither pedigree nor performance records tend to be kept (Marshall et al., 2019). The Dairy Genetics East Africa project aimed to discover the best crossbred for varying production systems across Kenya, determining crossbred composition by genotyping animals and collecting performance data. Results showed that high proportion exotic crossbreds only produced more milk than those with intermediate proportions of exotic genetics under the best production environments, whereas there was no significant difference under intermediate and poor production environments (Ojango et al., 2014). Assuming that crossbreds with a lower proportion of exotic genetics will perform better for economically important adaptation traits, these results suggest that under conditions other than the best production environments, crossbreeding strategies which maintain intermediate levels of exotic genetics are likely to outperform grading up strategies which result in high proportions of exotic genetics. This highlights the need to design crossbreeding strategies with clear objectives, considering multiple traits and that consider the specific production system.

In other cases, attempts to implement systematic crossbreeding strategies have been made, but not necessarily with evidence that the strategy implemented will result in the desired breeding goal. For example, in Senegal, government initiatives incentivise farmers to grade up to crossbred cattle with high proportion exotic genetics in order to increase productivity (Marshall et al., 2019). However results of the Senegal Dairy Genetics project, which again used genotypes to predict crossbred ancestry, found that although crossing local cattle with exotic breeds led to increases in profit compared to local breeds, the most desirable composition was 50% local and 50% exotic (Marshall et al., 2017). This highlights the need to consider the long-term effects of a crossbreeding strategy. These results suggest that the

first generation of the grading up strategy would result in animals which perform well, but after this it may result in drops of productivity.

In other cases, crossbreeding programmes have occurred on research stations, for example, the formation of the Mpwapwa composite in Tanzania. This composite was formed by crossing Red Sindi, Sahiwal, Tanganyika Shorthorn Zebu, Boran and European breeds (Kiwuwa and Kyomo, 1971) and by conducting breeding on a research station, it allowed recording of pedigrees and phenotypes, allowing a more systematic breeding strategy. However, distributing these cattle to the wider community has been challenging due to the small population size and so backcrossing to Boran and Sahiwal breeds has been used to increase population size (Chawala et al., 2017). Maintaining a complex crossbreeding strategy such as this would be impractical for a typical farmer, particularly if they have a small herd. This highlights the need to consider the practicality of implementation when designing crossbreeding strategies.

1.4.6 Predicting the performance of crossbreds

In order to assess a crossbreeding strategy, we need to be able to predict the performance of a range of crossbred individuals. This can be estimated using models considering the additive effects of the parental breeds, their proportions in the cross, as well as non-additive effects for the pair of parental breeds, with corresponding coefficients depending on the class of cross (e.g. F1, first backcross, F2 etc). Non-additive effects can include heterosis, recombination loss and maternal or paternal effects. A number of models have been suggested (Dickerson, 1969, 1973; Kinghorn, 1980; Grosshans et al., 1994; Wolf et al., 1995; Kahi et al., 2000b) to estimate the performance of crossbreds. When tested using data from

a crossbreeding study in Ethiopia, the Dickerson 1973 model performed the best (Demeke et al., 2003a) and has the added benefit of being less complex than other models.

Dickerson's model includes additive, heterosis and recombination loss effects. The mean performance of a class of cross can be estimated:

$$Performance_{ij} \sim \mathrm{alL} + \mathrm{aeE} + \mathrm{h}H_{le} + \mathrm{r}R_{le}$$

L and **E** are the additive effects of breeds l and e respectively, equal to the mean performance of the purebred animals of each breed.

H_{le} is the maximum heterosis effect of crossbreds of breeds l and e, caused by dominance effects. It is defined here as the difference between the performance of F1 individuals and the midpoint between the performance of the two parental breeds. It is usually positive because increased heterozygosity tends to lead to increased performance and the maximum heterozygosity will occur in the first cross.

R_{le} is the recombination loss effect of crossbreds of breeds l and e. This is caused by the breakdown of favourable epistatic blocks of genes from parental breeds. It is thought that this effect will be particularly pronounced in crosses of heavily selected breeds.

The coefficients al, ae, and h and r are dependent on the class of cross.

al is the proportion of breed l and **ae** is the proportion of breed e

h is dependent on the level of heterozygosity. The maximum heterozygosity is achieved in the F1 and reduces over time.

r is dependent on the amount of recombination possible between parental haplotypes. It is calculated as the mean fraction of independently segregating pairs of loci in gametes from both parents that are expected to be non-purebred. An example of how this is calculated can be seen below.

Sire: Breed 1 Genotype: A1A1 B1B1 Possible Gametes: A1B1 A1B1 A1B1 A1B1	**Dam:** F1 (Breed 1 x Breed 2) Genotype: A1A2 B1B2 Possible Gametes: A1B1 A1B2 A2B1 A2B2

Figure 1.1 Example calculation of r, the weight for recombination loss in the estimation of crossbred performance. In this example, the value of r is calculated for offspring resulting from a first backcross mating between a purebred sire of breed 1 and an F1 dam resulting from crossing breed 1 and breed 2. We consider a pair of loci, A and B, each with two potential alleles, 1 and 2, which originate from breeds 1 and 2. In order to calculate the value of r, the proportion of gametes with non-purebred pairings of alleles is calculated. In this example, all gametes from the sire are pairings which occur in the purebred. However, 2 out of 4 possible gametes produced by the F1 have pairs of alleles which do not occur in purebreds (A1B2 and A2B1). Therefore, for offspring of this mating, r will equal 2/8, or 0.25.

In order to estimate the crossbreeding effects (L, E, H and R) for a specific pair of breeds and trait, studies measure the performance of a range of classes of crossbreds (as well as the purebred breeds) and use the model to produce least square mean estimates. These can then be used to estimate the mean performance of a class of cross not measured.

1.5 Thesis outline and main objectives

The aim of this PhD is to assess the potential for crossbreeding strategies to increase productivity and profitability and decrease GHG emissions and emission intensity of cattle farming in SSA. To achieve this, the main objectives are:

1. To gain a greater understanding of the expression of additive and non-additive genetic effects in crossbred cattle in the tropics.

2. To predict the performance of crossbreds not only for production, but also for other important traits.
3. To predict the long-term effects of crossbreeding strategies on herd composition.
4. To predict how this varying herd composition affects productivity, profitability and GHG emissions.
5. To use these models to assess a range of crossing strategies for a specific exemplar case study system and consider how changes to that system may affect which strategy is optimal.

Chapter 2 describes a meta-analysis, exploring the effects of trait, breed pairing and environment on the expression of heterosis in cattle breeding in the tropics. The aim is to provide a greater understanding of this important non-additive genetic effect, and allow better design of crossing strategies that take advantage of heterosis.

Chapter 3 describes a model to predict the most important fertility parameters from others that are more commonly reported, allowing us to predict the number of calves born to varying crossbreds. This is necessary to predict herd dynamics under varying crossing strategies.

Chapter 4 describes a model to predict herd composition over time under varying crossbreeding strategies. The model uses Dickerson's genetic model to predict herd productivity for a case study of Holstein-Boran crossbreeding in Ethiopia.

Chapter 5 describes an extension to the herd model which predicts how varying crossbreeding strategies affect herd profit and GHG emissions over time. Again, this is tested using the Ethiopian case study.

Chapter 6 uses these models to test further crossbreeding strategies for the Ethiopian case study. A biological sensitivity analysis is also carried out to consider how varying genetic effects for survival affect the performance and ranking of crossing strategies.

Chapter 2: Heterosis in cattle crossbreeding schemes in tropical regions: Meta-analysis of effects of breed combination, trait type, and climate on level of heterosis

2.1 Chapter Introduction

The performance of a crossbred individual is not only dependent on the additive genetic effects from the breeds involved, but also the non-additive genetic effects. A particularly important non-additive is heterosis, usually defined in animal breeding as the difference in performance between that of the F1 and the mean of the two purebreds. In order to effectively design a crossbreeding strategy, we need to understand what factors have an effect on the amount of heterosis. This chapter uses a meta-analysis of cattle crossbreeding in the tropics to investigate how heterosis varies across different traits, depending on breed combination and environmental conditions, which are particularly important in tropical systems with diverse breeds and environments. This understanding helps to design strategies to best take advantage of heterosis, addressing the first objective of the thesis.

The body of the chapter has been published in the Journal of Animal Science. This student conducted all work related to this chapter under the guidance from her supervisors.

2.2 Manuscript

Heterosis in cattle crossbreeding schemes in tropical regions: Meta-analysis of effects of breed combination, trait type and climate on level of heterosis[1]

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Abstract

The aim of this study was to investigate the effects of animal trait, breed combination and climate on the expressed levels of heterosis in crossbreeding schemes using tropical cattle. A meta-analysis of 42 studies was carried out with 518 heterosis estimates. In total, 62.5% of estimates were found to be significantly different to zero, the majority of which (89.8%) were beneficial for the studied trait. Trait and breed combination were shown to have a significant effect on the size of heterosis ($p<0.001$ and $p=0.044$, respectively). However climate did not have a significant effect. Health, longevity and milk production traits showed the highest heterosis (31.84±10.73%, 35.15±3.29% and 35.13±14.35%, respectively), whereas fertility, growth and maternal traits showed moderate heterosis (12.02%±4.10%, 12.25%±2.69% and 15.69%±3.27%, respectively). Crosses between breeds from different types showed moderate to high heterosis ranging from 9.95±4.53% to 19.53±3.62%, whereas crosses between breeds from the same type did not express heterosis that was significantly different to zero. These results show that heterosis has significant and favourable impact on productivity of cattle farming in tropical production systems, particularly in terms of fitness but also milk production traits.

Key Words: crossbreeding, heterosis, meta-analysis, tropical cattle

Introduction

Heterosis is the difference in phenotype between the mean of crossbreds and their purebred parents (Notter et al., 2013). In animal breeding this is usually expressed as mid-parent heterosis or the superiority of the F1 cross over the mean performance of the two parents (Dickerson, 1969, 1973) and has been shown to occur across species (reviewed in: Sheridan, 1981). Deviations from the mid-parent value can be positive or negative but are mostly found to be beneficial (Powers, 1944). In cattle breeding, crossing has been used to take advantage of heterosis under a range of systems. In temperate systems, heterosis has been shown for fertility (Coffey et al., 2016), milk (Lembeye et al., 2016) and growth traits (Schiermiester et al., 2015). In the tropics a variety of crossing strategies have been implemented with varying levels of success (reviewed in: Mcdowell, 1985; Cunningham and Syrstad, 1987). The performance of these crosses is dependent on the expression of additive and non-additive genetic effects, particularly heterosis. To design an effective crossing strategy, it is important to understand how heterosis varies across different traits, depending on breed combination and environmental conditions, particularly in tropical systems with diverse breeds and environments. Meta-analyses are useful in aggregating results from a variety of studies and quantifying the effect of specific factors. In previous reviews without meta-analysis, the effects of specific factors were not able to be quantified and a limited combination of breeds and traits tended to be investigated (Syrstad, 1985). In the current study, we quantify the benefits of heterosis across studies and identify factors influencing heterosis, including the breed combination, trait type and climate. We also test heterosis globally to ensure results are not simply the effect of a specific set of experimental conditions, allowing more reliable parameter estimates for modelling (Sauvant et al., 2008).

Materials and Methods

Literature search

Crossbreeding studies which estimated heterosis effects were found from a literature search using Web of Science (ISI). The keywords heterosis AND cattle AND ["zebu" OR "sanga" OR "criollo" OR "indicus" OR "brahman"] were used and reference lists of the obtained articles were screened to find additional relevant papers, particularly those cited in key review papers (Mcdowell, 1985; Syrstad, 1985). A total of 134 articles were identified and screened. Articles were excluded if they did not include at least one tropically-adapted breed and did not contain the required data for analyses, including standard errors. After editing, 42 studies (Table 2.3) with 518 estimates were found to meet the criteria set and were retained for subsequent analysis.

Data extraction

The majority of studies contained multiple heterosis estimates for a variety of traits, breed combinations and environments. For each heterosis estimate the following values were recorded: the size of the effect, the standard error of the heterosis estimate and the mean performance of the purebred. In studies where the average parental purebred performance was not recorded it was calculated from the reported means for each purebred[1].

In addition, the breed combination, trait and location of study for each heterosis estimate were recorded in order to define the type of cross, trait and climate respectively. Breeds were sorted into three types, European *Bos taurus* (E), tropical *Bos taurus* (T) and tropical *Bos indicus,* also known as zebu (Z) (Table 2.4). There were six possible pairs of parental breeds (including crosses within and across types); however no studies were found of crosses between two tropical *Bos indicus* type breeds, meaning there were a total of five cross type categories: European *Bos taurus* x European *Bos taurus* (ExE), *Bos indicus* x *Bos*

[1] The mean performance for each purebred was exacted from the study and the mean of the two values was calculated.

indicus (ZxZ), tropical *Bos taurus* x European *Bos taurus* (TxE), tropical *Bos taurus* x *Bos indicus* (TxZ) and *Bos indicus* x European *Bos taurus* (ZxE). Traits were sorted into 11 types, including efficiency, fertility, growth, health, longevity, maternal[2], meat, milk, temperament, birth weight and other (Table 2.5). The location of the animals of the study was used to define the climate using the "Livestock Geo-Wiki" (Robinson et al., 2014), based on Robinson et al. (2011), as either arid and semi-arid tropics and subtropics, humid and sub-humid tropics and subtropics, or temperate and tropical highlands.

Statistical Analysis

In order to standardise heterosis values from different studies and traits these were expressed as a percentage of the mean performance of the two purebreds. Each estimate was multiplied by either 1 or -1, such that estimates in the desired direction for the trait were expressed as positive. The resulting values were used as the dependent variable in the model.

Following the guidelines for meta-analyses (Sauvant et al., 2008), each data point requires a measure of its reliability which is then used to weight it in the model. The standard error of an estimate is commonly used. However in the present study, the units of standard errors vary due to multiple traits being tested. In order to standardise our standard errors, we divided each by the original heterosis estimate to remove the units. The inverse of this standardised standard error was then used as weight in the analysis, meaning that estimates with large standard errors contributed less to the result. All weights were made positive and to avoid using weights of zero, where the mean heterosis was equal to zero the weight was made equal to 0.0001.

[2] Maternal ability traits, for example average daily weight gain of calf.

The following model was used to assess the impact of the three factors on heterosis:

$$Y_{ijk} = \mu + T_i + B_j + C_k + e_{ijk},$$

where Y_{ijk} was the standardised heterosis for a trait type i (i=1-11), between breed cross type j (j=1-5) and in climate k (k=1-3). Trait type, T, cross type, B, and climate, C, were fixed effects and e was the random error term. For simplicity, the weights are not shown but, as stated previously, each value of Y was weighted according to the inverse of the standardised standard error.

Results

The mean heterosis was 12.9% (median = 9.4%) with a standard deviation of 20.0%. Estimates ranged from -33.3 to 155.6%; among all estimates, 62.5% were found to be significantly different to zero (95% confidence interval). The majority of these showed beneficial heterosis but 6.4% of all estimates showed significant non-beneficial heterosis. Trait type and cross type were shown to have a significant effect on the size of heterosis ($p<0.001$ and $p=0.044$, respectively). However, climate did not have a significant effect.

Health, longevity and milk production traits showed the highest heterosis manifested by the largest least squares means, although the standard errors of estimates for health and longevity were also large (LSM = 31.84%±10.73%, LSM = 35.13%±14.35% and 35.15%±3.29%, respectively). Fertility, growth and maternal traits showed moderate heterosis (LSM = 12.02%±4.10%, 12.25%±2.69% and 15.69%±3.27%, respectively). The LSM heterosis of all other trait types was not significantly different to zero (95% confidence interval) (Table 2.1).

Crosses between tropically adapted *Bos taurus* and temperate *Bos taurus* breeds (TxE) showed the greatest heterosis (LSM = 19.53%±3.62) and crosses between zebu cross temperate *Bos taurus* breeds (ZxE) showed intermediate heterosis (LSM = 15.04%±2.92). Crosses between tropically adapted *Bos taurus* and zebu breeds (TxZ) showed the lowest

heterosis of a between type cross (LSM = 9.95%±4.53). The LSM of both within breed type crosses were not significantly different from zero (ExE = 8.22%±4.63 and ZxZ = 6.88%±10.81)(Table 2.2).

Discussion

Traits

Our results showed that health and longevity traits tended to show high heterosis whereas in meat traits much less heterosis was expressed. This supports the view that traits that are more closely related to evolutionary fitness show greater heterosis (Merilä and Sheldon, 1999), as health and longevity are more directly related to fitness than meat type traits. It is suggested that traits with lower heritability, such as fitness traits, may have higher heterosis effects as they are largely affected by dominance (Merilä and Sheldon, 1999). This pattern was also found in a crossbreeding study of sorghum plants, where traits showing low heritability, such as grain yield, tended to have higher heterosis compared to more heritable traits, such as plant height (Liang et al., 1972). Similarly, results of a meta-analysis of inbreeding depression in 6 livestock species found meat and temperament traits did not show significant inbreeding depression, whereas adult survival and fecundity did (Leroy, 2014).

We might expect milk production traits to behave similarly to other production traits, such as growth or meat traits, but our results show these milk traits tend to also show high heterosis, similar to that expressed in health and longevity traits. There may be a number of reasons for this. Firstly, we might consider milk production to be a fitness trait as it has an important effect on the survival of offspring. Therefore we might expect it to have high heterosis, as for health and longevity traits. Also, we expect fitness traits to show higher heterosis because they have been under long-term, intense, directional natural selection

(Merilä and Sheldon, 1999). In dairy cattle milk production traits have also experienced very intense directional selection. Studies of European cattle genotypes show evidence for selective sweeps where strong selection for a trait has resulted in all genes in a region having gone to fixation, particularly in regions we now know contain genes with a strong influence on milk production (Hayes et al., 2009). We might expect milk production traits to behave similarly to fitness traits as both have experienced this intense directional selection. In a meta-analysis, Leroy (2014) found that across livestock species, some production traits tended to show high levels of inbreeding depression, particularly milk production which is in line with our results, but also litter weight, which whilst less important in cattle, where litter size is usually one, may also have been under strong selection in other species, particularly pigs (Groenen, 2016). However in the study of Leroy (2014), birth weight was significantly affected by inbreeding depression, whereas we did not find any significant heterosis associated with birth weight. This may be due to the difference between species considered, especially since species such as pigs have large litters.

Breed combination

It is thought that genetic distance between parental breeds is very likely to have an effect on heterosis. One hypothesis is that increasing the genetic distance between breeds will increase the level of heterosis in their crosses. This can be explained by considering heterosis as the inverse of inbreeding depression, which occurs when two closely related individuals tend to have less fit offspring (Charlesworth and Charlesworth, 1987). The more distantly related parents are, the smaller the size of the inbreeding depression (Walling et al., 2011) which we could consider as an increased effect of heterosis. In a study of heterosis in protein production in yeasts, Blein-Nicolas et al. (2015) found that interspecies crosses (crosses with more genetically diverse parents) tended to show more positive heterosis (78.8%) than

intraspecies crosses (crosses with more closely related parents) (42.6 to 52.3%). A previous study of crosses of European dairy cattle breeds found increased heterosis in crosses where parental breeds are more distantly related (Gram and Pirchner, 2009) and this idea has been used in the past to predict heterosis using the genetic distance (Roughsedge et al., 2001).

Tropically-adapted cattle breeds are more distantly related than any of the breeds measured in previous cattle studies. In some cases, crosses of very distantly related strains can lead to outbreeding depression, where heterosis effects are negative (Lynch, 1991). An extreme example of this is crosses between two different species where offspring are often infertile (for example, Ålund et al., 2013).

If heterosis in tropical cattle breeding is occurring as the inverse of inbreeding depression, we expect crosses between more distantly-related breeds (TxE, ZxE and TxZ in the present study) to show more favourable heterosis than crosses between breeds of the same type (ZxZ and ExE). Conversely, if outbreeding depression is occurring, we expect crosses between different breed types (TxE, ZxE and TxZ) to show less favourable heterosis than crosses between breeds of the same type (ZxZ and ExE). Heterosis between distantly-related breeds may even be negative; meaning the performance of the F1 is less favourable than the mean parental performance. Our results support the first hypothesis than heterosis is the inverse of inbreeding depression as the heterosis in ExE and ZxZ crosses was found to be less favourable than that expressed by TxE, ZxE and TxZ crosses and the LS mean heterosis for all cross types was positive.

We can further group the three breed types in two different ways. Either according to sub-species type (*indicus* or *taurus*) or according to the climate for which they are adapted (temperate or tropical). If sub species were more important, we might expect crosses between breeds from the same sub species (TxE) to show lower heterosis than breeds from

different sub species (ZxE and TxZ). If climate adaptation were more important, we would expect crosses between breeds from the same climate (TxZ) to show lower heterosis than breeds from different climates (ZxE and TxE). Our results show that the lower heterosis for crosses between breed types was found in TxZ crosses, suggesting that diversity in climate adaption may be a better indicator for expected heterosis than the sub species classification. This may also suggest that tropically adapted taurine and zebu breeds are more closely related genetically than their classification might suggest.

There was large variation in the size of heterosis found in ZxZ crosses. This may suggest there is larger genetic diversity within this breed type as some crosses between closely related breeds expressed low levels of heterosis whereas others may be between more distantly related breeds and so express levels of heterosis closer to those found in crosses between different breed types. This is supported by a study of diversity of European and African cattle breeds, where although the average genetic distance between breeds from within each continent was similar (a mean Nei's genetic distance of 0.045 and 0.047 for breeds from Africa and Europe, respectively), the variation in genetic distance between breeds from Africa was larger than between breeds from Europe (a standard deviation of Nei's genetic distances of 0.029 and 0.013 for breeds from Africa and Europe, respectively) (Gautier et al., 2007).

Climate

Generally, more extreme climates are thought to lead to more extreme heterosis effects (Einfeldt et al., 2005; Penasa et al., 2010), potentially due to the increased importance of fitness traits in these environments. This is supported by a study that found inbreeding depression was greater in mice in the wild, compared to those kept in the lab where conditions were likely to be optimised (Jimenez et al., 1994). Tropical or arid environments

may increase stress as cattle are more likely to experience heat stress, reduced food and water availability and therefore we might expect heterosis to be greater than that found in temperate climate. However we did not find a significant effect of climate on heterosis in the present study.

Our climate measure may not be a good proxy for stress in cattle, as the majority of studies were conducted on research stations (39 out of 43), where we would expect conditions to be generally good, even under a harsher climate. There is also likely to be large variation in environment quality within each climate and this could explain why no effect of climate was found. Barlow (1981) carried out a review of heterosis x environment interactions and found many studies across a wide range of species where the expression of heterosis varied across different environments. In general, a poorer environment led to greater heterosis, except in the case of growth and fecundity traits where this pattern was less clear. However the authors also found problems with carrying out a strict meta-analysis due to variation in environment conditions across studies and results are instead simply displayed as subjective tabulation.

Within a number of the studies included in our analyses, multiple environments were tested. In one study of Angus Brahman crosses heterosis in a range of maternal traits was found to be greater when animals had poorer quality grazing (Brown et al., 1997). Similar results were found for milk production and somatic cell count (Brown et al., 2001). However no differences were found between grazing type for heterosis in a range of growth traits (Brown et al., 1993).

Conclusion

Results from the present study show that the type of trait and the combination of breed types both have a significant effect on the expression of heterosis. Heterosis was found to be

beneficial for a range of economically important traits, including those related to fitness such as fertility and longevity, which are particularly important in low input systems common in the tropics. The most beneficial heterosis was found for milk production traits which is useful to farmers as it is directly linked to income. Crosses of breeds of different types expressed greater beneficial heterosis than those of breeds of the same type. The greatest heterosis was expressed in crosses of breeds adapted to different environments, rather than crosses of breeds which have been considered to be from different sub-species. These crosses of breeds adapted to different environments dominate in the tropics as they allow the combination of complementary production and fitness traits, meaning that there is great potential to utilise heterosis to increase profitability. Outcomes of the present study highlight and quantify the benefits of heterosis in crossbreeding as a tool to improve profitability of cattle farming in the tropics.

Tables and Figures

Table 2.1. Least squares means and standard error of heterosis estimates (%) for trait type effect

Trait type	N[1]	Least squares mean[2]	Standard error
Birth Weight	72	-0.42[a]	3.12
Efficiency	3	0.96[abc]	19.00
Meat	48	6.07[ab]	4.17
Temperament	2	-18.82[ab]	13.22
Other	9	1.33[ab]	10.25
Fertility	40	12.02[ab]	4.10
Growth	185	12.25[b]	2.69
Maternal	62	15.69[b]	3.26
Health	6	31.84[abc]	10.73
Longevity	2	35.13[abc]	14.35
Milk	89	35.15[c]	3.29

[1]Number of heterosis estimates for each level of the type trait effect

[2]Means without the same superscript letter differ significantly, P< 0.05

Table 2.2. Least squares means and standard error of heterosis estimates (%) for breed type effect

Breed type[1]	N[2]	Least squares mean[3]	Standard error
ExE	65	8.22[a]	4.64
TxE	80	19.53[a]	3.62
TxZ	23	9.95[a]	4.53
ZxE	332	15.04[a]	2.92
ZxZ	18	6.88[a]	10.81

[1]European *Bos taurus* x European *Bos taurus* (ExE), *Bos indicus* x *Bos indicus* (ZxZ), tropical *Bos taurus* x European *Bos taurus* (TxE), tropical *Bos taurus* x *Bos indicus* (TxZ) and *Bos indicus* x European *Bos taurus* (ZxE).

[2]Number of heterosis estimates for each level of the breed type effect

[3]Means without the same superscript letter differ significantly, $P < 0.05$

Table 2.3 List of studies included in analysis with locations of animals and crosses included in each study.

Study	Locations	Crosses
(Akah, 1992)	Legon, Ghana	Sokoto Gudali x Jersey West African Shorthorn x Jersey
(Arce, 2006)	Texas, USA	Nellore x Angus
(Arthur et al., 1999)	Ebor, Australia Grafton, Australia Mummulgum, Australia NSW, Australia	Hereford x Brahman
(Arthur et al., 1994)	Ebor, Australia Grafton, Australia	Hereford x Brahman
(Birhanu et al., 2015)	Ethiopia	Boran x Holstein Friesian
(Boenig, 2011)	Texas, USA	Hereford x Brahman
(Brown et al., 2001)	Arkansas, USA	Angus x Brahman
(Brown et al., 1997)	Arkansas, USA	Angus x Brahman
(Brown et al., 1996)	Arkansas, USA	Angus x Brahman
(Brown et al., 1993)	Arkansas, USA	Angus x Brahman
(Brown et al., 2000)	Arkansas, USA	Angus x Brahman
(Chase et al., 1998)	Florida, USA	Hereford x Senepol
(Demeke et al., 2003b)	Ethiopia	Barca x Friesian Barca x Jersey Barca x Simmental Boran x Friesian Boran x Jersey Boran x Simmental Horro x Friesian Horro x Jersey Horro x Simmental
(Demeke et al., 2004a)	Ethiopia	Boran x Friesian Boran x Jersey
(Demeke et al., 2000)	Ethiopia	Boran x Holstein Friesian
(DeRouen et al., 1992)	Louisiana, USA	Angus x Brahman Angus x Charolais Angus x Hereford Brahman x Charolais Brahman x Hereford Charolais x Hereford
(Elzo et al., 2012)	Florida, USA	Angus x Brahman
(Franke et al., 2001)	Louisiana, USA	Angus x Brahman Angus x Charolais Angus x Hereford Brahman x Charolais

		Brahman x Hereford Charolais x Hereford
(Haile et al., 2009b)	Ethiopia	Boran x Holstein Friesian
(Hirooka and Bhuiyan, 1995)	Bangladesh	Bangladesh zebu x Holstein
(Kahi et al., 2000a)	Coast Province, Kenya	Ayrshire x Brown Swiss Ayrshire x Sahiwal Brown Swiss x Sahiwal
(Kahi et al., 1995)	Coast Province, Kenya	Ayrshire x Brown Swiss Ayrshire x Sahiwal Brown Swiss x Sahiwal
(Key, 2004)	Texas, USA	Brahman x Angus Brahman x Hereford
(Lema et al., 2011)	Paysandú, Uruguay	Hereford x Angus Hereford x Nellore Hereford x Saler
(Lemos et al., 1992)	South Eastern Brazil	Holstein Friesian x Guzera
(Mackinnon et al., 1996)	Kilifi, Kenya	Sahiwal x Ayrshire
(Magaña and Segura, 2003)	Yucatan, Mexico	Brahman x Commercial Zebu Brahman x Gyr Brahman x Indubrazil Commercial Zebu x Gyr Commercial Zebu x Indubrazil Indubrazil x Gyr
(Menéndez Buxadera and Ayrado, 2013)	Cuba	Zebu x Holstein
(Osorio-Arce and Segura-Correa, 2010)	Tabsaco, Mexico	Brahman x Brown Swiss Brahman x Charolais Brahman x Simmental
(Rege et al., 1994)	Legon, Ghana	Jersey x Ghana Shorthorn Jersey x Sokoto Gudali
(Riley et al., 2016)	Arkansas, USA	Angus x Romosinuano
(Riley et al., 2014a)	Florida, USA	Angus x Brahman Romosinuano x Angus Romosinuano x Brahman
(Riley et al., 2014b)	Florida, USA	Angus x Brahman Romosinuano x Angus Romosinuano x Brahman
(Riley et al., 2007)	Florida, USA	Angus x Brahman Romosinuano x Angus Romosinuano x Brahman
(Riley et al., 2010)	Florida, USA	Angus x Brahman Romosinuano x Angus Romosinuano x Brahman
(Riley et al., 2015)	Arkansas, USA	Angus x Romosinuano
(Roberson et al.,	Texas, USA	Hereford x Brahman

1986)		
(Schoeman et al., 1993)	South Africa	Afrikaner x Hereford Afrikaner x Simmentaler Simmentaler x Hereford
(Sharma and Pirchner, 1991)	India	Sahiwal x Holstein Friesian
(Sharma et al., 2000)	India	Sahiwal x Holstein
(Skrypzeck et al., 2000)	Hohannesburg, South Africa	Afrikaner x Hereford Afrikaner x Simmentaler Simmentaler x Hereford
(Theunissen et al., 2015)	South Africa	Afrikaner x Brahman Afrikaner x Charolais Afrikaner x Hereford Afrikaner x Simmentaler Charolas x Brahman Charolais x Hereford Charolasi x Simmentaler Hereford x Brahman Hereford x Simmentaler Simmentaler x Brahman

Table 2.4. Frequency of heterosis estimates for all breeds found across all studies and their classification into three breed types: temperate *Bos taurus*, tropical *Bos taurus* and *Bos indicus*.

Breed	**Frequency**
Bos indicus	391
Arsi	2
Bangladesh zebu	2
Barca	12
Boran	38
Brahman	225
Commercial Zebu	9
Guzera	2
Gyr	9
Horro	12
Indubrazil	9
Nellore	8
Sahiwal	37
Sokoto Gudali	25
Zebu	1
Temperate *bos taurus*	542
Angus	152
Ayrshire	16
Ayrshire and Brown Swiss	5
Ayshire	4
Brown Swiss	18
Charolais	51
Friesian	18
Hereford	129
Holstein	10
Holstein-Friesian	27
Jersey	68
Saler	2
Simmental	14
Simmentaler	28
Tropical bos taurus	103
Afrikaner	28
Ghana Shorthorn	12
Romosinuano	39
Senepol	11
West African Shorthorn	13

Table 2.5. Frequency of heterosis estimates for all traits found across all studies and their classification into eleven trait types: birth weight, efficiency, fertility, growth, health, longevity, maternal, meat, milk, temperate and other.

Trait	Frequency
Birth Weight	72
Birth weight	68
Female birth weight	2
Male birth weight	2
Efficiency	3
Daily feed intake	1
Days on feed	1
Ratio gain:daily feed intake	1
Fertility	40
Age at first calving	12
AI success	1
Calving interval	12
Calving rate	10
Days open	1
Services per conception	4
Growth	185
Average daily gain	22
Cow weight	22
Heifer height	1
Heifer weight	24
Preweaning average daily gain	22
Preweaning body condition score	3
Steer liveweight	5
Weaning age	3
Weaning height	10
Weaning weight	57
Weaning weight / wenaing height	4
Yearling weight	12
Health	6
Calf survival rate	2
Somatic cell count	4
Longevity	2
Total lifespan	1
Total productive lifespan	1
Maternal	62
Calf average daily gain	3
Calf body condition score	3
Calf height	2
Calf survival	3
Calf weaning height	4

Calf weaning rate	6
Calf weaning weight	10
Calf weaning weight per cow exposed	15
Cow efficiency (weaning weight / cow weight at calving) x (365/CI)	3
Cow productivity (weaning weight x 365/CI)	3
Cow weight change during lactation	1
Ratio calf weaning weight:cow weight	1
Ratio Calf weight:height	4
Ratio cow weight change:calf weight change	1
Ratio weaning weight:calving interval	3
Meat	48
Connective tissue score	1
Dressing percentage	1
Fat percentage on kidney, pelvic & heart	1
Fat thickness	6
Fat tickness over ribeye	1
Flavour score	1
Hot carcass weight	7
Juiciness score	1
Marbling score	7
Muscle area of longissimus	6
Muscle area of ribeye	1
Off flavour score	1
Retail yield	6
Tenderness score	1
Warner - Bratzler shear force	7
Milk	89
300-day yield	1
305-day yield	1
Annualized yield	9
Average daily yield of productive life	1
Average daily yield of total life	1
Daily yield	19
Dry period	3
Fat percentage	8
Lactation fat yield	4
Lactation length	14
Lactation yield	17
Lifetime yield	3
Protein percentage	4
Ratio annual milk yield:body weight	2
Ratio Yield:calving Interval	2
Temperament	2
Chute exit velocity	2
Other	9
Final body weight	1
Initial age	1

Initial body weight	1
Julian birth date	6
Total	518

2.3 Chapter conclusion

Results of this chapter show the huge potential to increase performance for desirable traits by designing crossbreeding strategies that take advantage of heterosis. Traits that have an important impact on the efficiency of a farm, such fertility, health and longevity were found to show moderate to high beneficial heterosis, suggesting that a well-designed crossbreeding strategy could lead to more efficient systems. In addition, the large beneficial heterosis seen for milk production traits is particularly favourable because increasing milk production will directly increase productivity and income for farmers. An increase in milk production per individual is also likely to reduce milk GHG emission intensity of the system.

As the greatest heterosis was seen between breeds that are adapted for different environments, crossbreeding strategies that uses a local tropical breed and an exotic temperate breed are likely to be successful. These two breed types are diverse in terms of the traits for which they perform well. Local breeds tend to perform best for adaptation but poorly for productivity traits, whereas exotic breeds tend to perform best for productivity but poorly for adaptation traits. The significant beneficial heterosis for these traits which is predicted by the results of this meta-analysis means that local x exotic crossbreds should perform significantly better for both adaptation and production traits compared to the average of the purebreds, leading to a more productive, profitable and environmentally efficient system.

Therefore, in the remaining chapters, crossbreeding strategies which use a local tropical and an exotic temperate breed will be modelled and tested for cattle farming systems in SSA. Parameters from studies including in this meta-analysis will as inputs for these models.

Chapter 3: Predicting age-specific calving rates from age at first calving and calving interval in cattle

3.1 Chapter Introduction

In order to model how the composition of a herd changes over time, we need to predict calving rates of different animals at different ages. As this thesis aims to model the effects of crossbreeding strategies, we specifically need to model how different crossbred individuals vary in terms of their probability of calving at different ages. As described in chapter 1, Dickerson's model (Dickerson, 1973) can be used to predict the performance of different crossbred individuals for a given trait, using additive, heterosis and recombination loss parameters which have been estimated for that trait and specific breed pair and system from crossbreeding studies. However, results of the meta-analysis in chapter 2 show that despite these parameters being estimated for a range of fertility traits, they are not estimated specifically for age-specific calving rates. The most commonly reported fertility traits are age at first calving (AFC) and calving interval (CI).

Therefore, the aim of this chapter is to produce and test a model which uses AFC and CI to predict age-specific calving rates. Dickerson's model can then be used to predict AFC and CI for a range of crossbred individuals and these used to predict age-specific calving rates, which can be used as inputs for subsequent models in this thesis. It also addresses the second objective of the thesis by allowing the modelling of variation in a trait not directly linked to production, but linked to adaptation and one that will have an important impact on the efficiency of the system.

The body of the chapter has been submitted for publication and is under review by animal. This student conducted all work related to this chapter under the guidance from her supervisors and other co-author.

3.2 Manuscript

Predicting age-specific calving rates from age at first calving and calving interval in cattle

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Short title: Evaluating models to predict calving rates

Abstract

In order to model herd dynamics and profitability over time, age-specific calving rates are needed. However, particularly in areas where data are scarce, for example sub-Saharan Africa, few fertility traits are reported, most commonly age at first calving and calving

interval. Therefore we described and evaluated three models designed to translate age at first calving and calving interval into age-specific calving rates. Models were tested, by first using input parameters from Ethiopia and predicted calving rates were compared to those predicted using a stochastic simulation, and second by using input parameters from UK dairy cattle and predicted calving rates were compared to observed calving rates for the population. All three models performed well under both scenarios (R^2 from 0.98-1.00), with the model in which estimation errors were reduced by reducing the size of age class considered, performing the best. The models are useful when evaluating the profitability impacts of a breeding or management strategy which influences calving interval and age at first calving.

Key words: fertility, herd profitability, farm systems modelling, calving patterns, calving rate

Implications

A model to efficiently and accurately predict age-specific calving rates across the life of a cow from the mean and standard deviation of the age and first calving and calving interval was evaluated. The model is useful when evaluating the profitability impacts of a breeding or management strategy which influences calving interval and age at first calving.

Introduction

When designing a breeding strategy it is important to consider the effects of not just production but also fitness traits, especially fertility, on the profitability of the farm (Pryce and Veerkamp, 2001). The impact of fertility on profitability is a long-term dynamic issue. Increasing the calving rate, that is the number of calves born within a given time period, has a direct impact on the farm profit, as each calving produces a calf, which itself has value and marks the beginning of a new lactation. Calving rates are known to vary across the lifetime of an animal (Osoro and Wright, 1992; Evans *et al.*, 2006).

In the tropics, local breeds are often crossed to exotic breeds to increase production levels (Cunningham and Syrstad, 1987). However animals with a high proportion of exotic compared to tropically-adapted breed genetics have been shown to perform poorly for a range of fertility traits in tropical climates, for example artificial insemination success rate (Menéndez Buxadera and Ayrado, 2013), pregnancy status (Olson *et al.*, 1990), age at first calving, days open and calving interval (Negussie *et al.*, 1999). Fertility traits also tend to show significant positive heterosis in cattle crosses in the tropics (Bunning *et al.*, 2019), meaning that modelling the results of crossing strategies cannot be done simply by linear combination of additive effects. Therefore multigenerational crossbreeding studies are needed to predict the fertility performance of a given crossbred type.

In order to model how crossbreeding strategies may affect herd profit in terms of fertility, age-specific calving rates are needed for different crossbreds. However the appropriate data needed to calculate these parameters are scarce, as long-term crossbreeding studies are impractical and costly. More commonly reported fertility traits include age at first calving (AFC) and calving interval (CI), often as an average across ages of animal (Bunning *et al.*, 2018).

The objective of this paper was therefore to evaluate some alternative methodologies for translating performance values for AFC and CI into probabilities of calving within each cow year of life for a herd with an all-year-round pattern of calving.

Materials and Methods

Three variations of a deterministic model were developed, with alternative approximation methods for parameters required to implement the model. Model 1 estimated that the mean of a section of a normal distribution is equal to the mid-point of the section. Model 2 reduced the error associated with this assumption by reducing the size of each age class and

so the size of the section of the normal distribution. Model 3 attempted to estimate the actual mean of the section. Differences among these Models are illustrated in Figure 1. These models were tested by comparing predicted calving rates to those derived from a stochastic simulation and, where possible, to observed values.

In a farm system model, total profit is a function of vector c, where c is the vector of total probability (across k parities) that a cow will calve within a set of n age classes where n is the maximum number of age classes that a cow could possibly calve in, given that she is still alive. Our aim was to derive and evaluate c from means and standard deviations of AFC and CI for a particular population.

We partitioned c into a series of sub vectors, each corresponding to a parity k, so that

$$c = \sum_{k} c_k$$

For parity k = 1

$$c_i^{k=1} = \int_{i-1}^{i} N\left(\frac{\mu_{AFC}}{w}, \frac{\sigma_{AFC}}{w}\right)$$

where N(μ, σ) denotes a normal distribution of first calving ages with mean μ and standard deviation σ, i is the age class of the current calving with each age class having a duration of w days, μ_{AFC} is the mean age at first calving in days, and σ_{AFC} is the standard deviation of age at first calving in days.

For subsequent parities (k>1) the probability of calving in any age class was dependent on the distribution of calvings across age class of the previous parity (k-1).

$$c_i^{k>1} = \sum_{j} q_{i,j,k} c_j^{k-1}$$

where $q_{i,j,k}$, the probability of a cow calving in age class i to start parity k, given that she last calved in age class j was calculated as

$$q_{i,j,k} = \int_{i-1}^{i} N(s_{j,k-1} + \frac{\mu_{CI}}{w}, \frac{\sigma_{CI}}{w})$$

where $s_{j,k-1}$ is the mean calving age measured in age class units (1 age class unit = w days) which corresponds to the previous age class of the calving (j) in the previous parity (k-1).

The calculation of $s_{j,k-1}$ varied across models, μ_{CI} is the mean calving interval in days, and σ_{CI} is the standard deviation of calving interval in days. For models 1 and 2, we made an approximation for the mean age of the previous calving as follows,

$$s_{j,k-1} = j + 0.5$$

so that $s_{j,k-1}$ is the midpoint of the age class of the previous calving. This special case means that the probabilities $q_{i,j,k}$ were identical across successive parities (i.e. across the dimension k).

The difference between models 1 and 2 was the size of w. In model 1, w = 365 days whereas in model 2, w = 36.5 days so that estimation errors using the midpoint rather than the mean calving age for the previous calving were reduced. In order to compare results between the models, for each age class 1 year in model 1, 0.1 year in model 2) values of c_i that fall within this model 1 age class, were summed.

In model 3, w = 365 days and the value taken for $s_{j,k-1}$ depends on the distribution within the age class at the previous calving and was derived using formulae to calculate means of sections of a normal distribution (Sandon, 1961) as below

$$s_{j,k-1} = \frac{1}{\left[\int_{-\infty}^{\frac{j-\mu_{k-1}}{\sigma_{k-1}}} N(0,1) - \int_{-\infty}^{\frac{j-\mu_{k-1}-1}{\sigma_{k-1}}} N(0,1)\right]}$$

Where μ_{k-1} and σ_{k-1} are the mean and standard deviation of age of calving for parity k-1.

$$\mu_{k-1} = \sum_{j} c_j^{k-1}(j + 0.5)$$

$$\sigma_{k-1} = \sqrt{\sum_j c_j^{k-1}(j+0.5)^2 - {\mu_k}^2}$$

Model testing

A stochastic simulation was used to test these three models. A data set of 100,000 individuals with values of AFC and 1st – 19th CI was simulated so that the mean and standard deviation of AFC and CI were equal to input parameters derived from two contrasting performance environments (Ethiopia and UK). Calving dates were then calculated for each individual. The number of calvings occurring within each of the 20 age classes was divided by the total number of individuals to calculate age class calving percentages. This was repeated 50 times and an average across replicates was estimated.

Ethiopian Cattle

To test the effectiveness of these models and compare results to those from the simulation, input parameters from a survey of farms in the Oromiya region of Ethiopia (Ayalew *et al.*, 2004) were used (Table 3.1). The associations between the predicted calving rates from each of the three models and the values from the simulation were measured by the coefficient of determination (R^2). The three models were also evaluated for bias by calculating the regression slope between their values and the values from the simulation. Finally, the mean absolute error (MAE) was also determined for each model compared to the simulation, which is calculated by finding the mean absolute difference between the predicted values from the model and those from the simulation. MAE is in the same units as the calving rates.

UK Dairy Cattle

We also tested the models using data from UK dairy cattle where individual calving records were also available through milk recording databases. Data consisted of calving records of UK Holstein cows born between 2002 and 2007. Only individuals with records of all of the

first 5 calving dates were included, resulting in a data set of 322,328 animals. These data were divided in half by randomly assigning each individual to either the training or testing set. From the training dataset the input parameters required for the models, the mean and standard deviation of AFC and CI, were calculated (Table 3.1). These parameters were used in models 1-3 and the simulation. The number of parities within the models was limited to 5. The actual calving percentages for each age class were then calculated from the test dataset and compare to the predicted values from models 1-3 and the simulation.

The associations between the predicted values from each of the three models and simulation, and the observed values from the data were measured by the coefficient of determination (R^2). The results from the models and simulation were also evaluated for bias by calculating the regression slope between their values and the observed values. Finally, the MAE was also determined for each model and the simulation, which is calculated by finding the mean absolute difference between each pair of predicted and observed values, measured in the same units as the calving rate.

UK Dairy seasonal calving herds

To create a data set of seasonally calving herds, a subset of the full UK dairy data set was created which only included animals from herds with 4 or fewer months with 10 or more calvings. This reduced the data to 9,251 individuals, each with 5 calving records. As before, the population parameters were calculated and used as inputs for the 3 models and simulation (Table 3.1). The predicted calving percentage for each age class was then compared to the actual calving percentages calculated from the data. As before, the results of models and simulation were compared to the observed values using the R^2, regression slope and MAE.

Results

Ethiopian Cattle

The predicted calving rates using the Ethiopian input parameters were very similar across all three models and the simulation (Table 3.2). The results from Model 2 were the most consistent with those from the simulation (regression slope = 1.000, R^2 = 1.000, MAE = 0.0000).

Annual calving rates were zero for animals up to 2 years old. A small proportion of animals (7%) were predicted to calve between the ages of 2 and 3 years old. Over 50% of animals were predicted to calve between the ages of 3 and 4 years, which aligns with the mean age at first calving of 3.89 years. The predicted calving rate from all the models fluctuated slightly but plateaued to an annual calving rate of 65% for all age classes over 8 years. This means that for any female that is alive over the age of 8, there is a 65% chance she will calve in a year.

UK Dairy Cattle

Again the results from all three models and the simulation were very similar. All were able to predict well the actual calving percentages for the testing data set using input parameters from the training data (Table 3.3). Predicted values from Model 2 and the simulation were most similar to observed values (Model 2 regression slope = 1.0113, R^2= 0.9955, MAE = 0.0200, Simulation regression slope = 1.0111, R^2= 0.9956, MAE = 0.0200).

For the main calving period (from ages 2 – 7 years) Models 1 and 3 tended to overestimate the calving percentages, but after this they underestimate calving percentages. At very young ages, all models overestimated calving percentage and at very old ages, all models underestimated calving percentage.

UK Dairy seasonal calving herds

The prediction ability of the models and simulation in this scenario was barely reduced compared to that for the full UK dairy data (Table 3.4). Again, Models 1 and 3 tended to slightly overestimate calving percentage during the peak and then underestimated during the later ages. Compared to the full UK dairy data, in this scenario, all models more accurately predicted the calving percentages at early ages. However, as before, at the older end, all models underestimated calving percentages.

Discussion

Our results show that all three models evaluated here successfully translated performance values for AFC and CI into probabilities of calving within each year of life. When tested against either a stochastic simulation and with input parameters from Ethiopia, or against observed values with input parameters from the UK, all three models performed well. Across all input parameters used, and under all methods of evaluation used, Model 2 performed the best.

Comparison of models

Models 1-3 differed in the methods of estimating mean age calving in a given age class for the previous parity ($s_{j,k-1}$). Model 1 estimated this simply to be the midpoint of the age class, introducing bias. For example, in Figure 3.1, in age classes below the modal age class, which is 1-2 years here, the mid-point of the age class (marked with a dotted line and Model 1 label) is lower than the true mean calving age in the class (marked with a dotted line and Model 3 label). This means model 1 will under estimate calving ages, meaning a greater chance for more calvings within a time period and so an over estimation of calving rates at these younger ages. In age classes above the modal age class, for example 3-4 years, the mid-point (marked with a dotted line and Model 1 label) is above the mean calving age in the class (marked with a dotted line and Model 3 label). Here model 1 will over estimate

calving ages, meaning less time for calvings within a time period and so an under estimation of the calving rates at older ages.

Although we measured this bias when comparing the predicted and actual values of calving rates for UK dairy cattle, the size of this bias was quite small (regression slope = 0.92, relative to an expectation of 1 with no bias). Model 2 reduced the size of this error by reducing the size of age classes to 0.1 years. This was successful as the bias was reduced (regression slope = 1.0), as well as MAE (0.02). Reducing the size of age classes further would increase the accuracy of the model, however it also increases the computational power needed. Model 3 attempted to reduce the error by estimating the mean age of calving for each age class rather than using the mid-point. For parities greater than 1, this estimation relies on the estimation of the mean and standard deviation of age of calving at the previous parity. From our results, these estimations produced a less accurate model than Model 2.

Comparison of results

The predicted annual calving rates for Ethiopia increased from zero for the first two years of a cow's life and then plateaued from about 4 years to the maximum age modelled because potential number of parities is not limited. The UK Holstein calving rates increased up to about 5 years of age and then decreased again until by 10 years old, calving rates were approximately zero. This is due to all animals in the data having 5 parities.

The maximum annual calving rate for UK Holsteins was predicted to a bit less than 1 (annual calving rate = 0.9 at 2-3 years) because the average calving interval was a small amount longer than 1 year (412 days) with a relatively small standard deviation, meaning many animals calved every year. The predicted maximum annual calving rate for cattle in Ethiopia was much smaller (around 0.65) because the mean calving interval is larger (562 days). We might expect the maximum annual calving rate to be equal to 365 days divided by the mean

CI and this was the case for the predicted rates in Ethiopia (365 days / 562 days=0.65). However the predicted annual calving rates for UK Holsteins peaked at 0.9, which is slightly greater than expected (365 days / 412 days=0.89). This was due to the variation in AFC, meaning that in the age class between 2 and 3 years, whilst some animals were calving for the first time, others were in their second parity, which increased the total number calving to slightly above what we might expect.

Predicted time taken to reach the approximate maximum calving rate was much less in the UK Holsteins (around 2 years), compared to the Ethiopian cattle (around 4 years). This is because the average age at first calving for the UK Holsteins was about 2.4 years whereas it was about 3.9 years for the Ethiopian cattle.

Model assumptions

An assumption of these models was that AFC and CI are normally distributed. This is not the case when herds calve seasonally, where calving age and interval distributions are often multimodal. This is because the aim is for all cows to calve at the same time of year. For example, in pasture systems, this allows farmers to take advantage of the most nutritious grass when cows' milk yield, and so nutrient requirements, are greatest (Cummins *et al.*, 2012). Assuming that in this system all calves are born at a very similar time in a given year, this means that cows in this system will have a very narrow range of AFC in a given year, leading to a multimodal distribution with the first peak at the ideal AFC and then further smaller peaks separated by multiples of one year. In order to test whether our models would work in seasonally calving systems, we reduced the UK dairy data and only selected herds which had the majority of calvings across a limited number of months (up to only 4 months with more than 10 calvings). This created a non-normal distribution of AFC (Figure 3.2). However the performance of the models did not change dramatically under any of the

measures of goodness of fit, suggesting that this deviation from the modelled normal distribution did not have a large effect on the goodness of fit of the models.

We also assumed no correlation between CIs for each parity for an individual as well as between an individual's AFC and CIs. Estimates of correlations between AFC and CI vary in the literature. In Iranian Holsteins, Faraji-Arough *et al.* (2011) report genetic and phenotypic correlations close to zero between AFC and both the first and second CI. However, in crossbred Colombian beef cattle, Vergara *et al.* (2009) report a moderate positive genetic correlation with a large standard error between AFC and both the first and second CIs. Between the first CI and AFC, they also report a moderate positive phenotypic correlation with a small standard error. However the phenotypic correlation found between AFC and second CI was small. Reported estimates of correlations between CIs for each parity tend to vary less. In crossbred Colombian beef cattle, a large positive genetic correlation, but only a small positive phenotypic correlation, were found between first and second calving interval (Vergara *et al.*, 2009). A similar trend was reported for Iranian (Faraji-Arough *et al.*, 2011) and Australian (Haile-Mariam *et al.*, 2003) Holsteins.

If our models were used to predict calving rates for a group of animals with high correlations between any of these traits, we might expect that the model would be a poorer fit. In particular, high correlations between CIs would mean that individuals that had lower CIs, would tend to have all theirs calvings, from the second parity onwards, earlier than other individuals and earlier than we would predict under the assumption of no correlation. This means a positive correlation between CIs would increase the calving rate from around the average age of second calving (equal to mean AFC plus mean CI), compared to predicted values where no correlations were assumed. The size of this increase would increase with larger positive correlations. In the UK Holstein data used to test our model, there were

significant but small correlations between CIs of different parities (0.11-0.18). However, we did not see an underestimation of calving rates around the average age of second calving. Either the observed correlation was not large enough to significantly affect the predictive ability of our models, or perhaps any underestimation was balanced or compensated for by other model properties which led to an equivalent overestimation.

Another assumption of the model was that there is no consistent change in CI across parities. In dairy cattle, the average CI tends to increase with increasing parity (Hare *et al.*, 2006). In US Holsteins, the average CI increased from 402.9 days for the first CI, to 412.9 days for the seventh. The rate at which CIs increase tends to increase, with the first few CIs tending to be similar and the later intervals being increasingly larger. This means that when modelling a system with a limited number of parities, this change in CIs will not be very large, meaning that the simple assumption of static CI is unlikely to cause prediction problems. However if we use these models for systems with parities greater than 5, we are likely to be overestimating calving rates later in an animal's life. In the UK Holstein population used to test our models, average CI increased from 408.7 days for the first interval, to 420.7 days in the fourth interval. This magnitude of increase over a system limited to 5 parities did not appear to have a large effect on the predictive performance of the models. However in a system with a larger change in CI over parities and with a larger number of potential parities, the performance of our models may decrease. It would be possible to include into our models distinct CI input values for each successive parity. However the aim of these models was to predict calving rates from a small number of input parameters and so this wasn't deemed necessary.

Finally, an important note is that our models assumed that fertility is independent of survival. The calving rates predicted here are equal to the probability a cow will give birth in

a specific year of life, given that she is alive during that year. These values can then be combined with survival probabilities (the probability a cow will survive to a specific year of age) to estimate total herd fecundity. On many farms, animals with consistently low fertility (i.e. large AFC or CIs) are often culled (Sewalem *et al.*, 2008), meaning that fertility and survival are not independent. However, our fertility models assumed that there was no consistency of CI length within an individual and across parities. Therefore these animals being more likely to be removed from the herd should not have influenced our results. Across a range of studies (including US Holsteins (Dematawewa and Berger, 1998), Czech Holsteins (Zavadilová and Zink, 2013) and Irish Holstein in a pasture-based system (Olori *et al.*, 2002)), phenotypic correlations between CI and survival were close to zero. As both our models and a survival model are concerned with phenotypic values, this suggests that an assumption of independence of fertility and survival may be valid.

Conclusion

When comparing model predictions against both simulated and observed values, all 3 models presented here worked well, with Model 2, which used small sized age classes, performing the best. Although designed initially to predict the performance of different crossbreds, these models are useful in any situation where the effect of any breeding or management strategy on AFC and CI is known. Our models can therefore be used to predict the effect of this strategy on age-specific calving rates, which can then be directly used to predict the effect of the strategy on profitability and inform breeding and management decisions.

Acknowledgments

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Tables and Figures

Table 3.1 Input parameters used to predict calving rates (including mean and standard deviation (SD) of age at first calving (AFC) and calving interval (CI)) for each population of cattle tested expressed in days.

Population	Mean AFC	SD AFC	Mean CI	SD CI
Ethiopia	1420	223	562	157
UK Dairy	888	143	412	82
Seasonally calving UK	885	171	402	81

Table 3.2. Predicted annual calving rates across age classes for cattle in Ethiopia. Linear regressions were used to compare results from each model to the simulation results. The regression slope and R^2 results of each analysis are presented alongside the mean absolute error (MAE) when comparing the model and simulation results. In all regressions there were no significant intercept effects.

	Annual Calving Rates			
Age Class (years)	Model 1	Model 2	Model 3	Simulation
0 – 1	0.00	0.00	0.00	0.00
1 – 2	0.00	0.00	0.00	0.00
2 – 3	0.07	0.07	0.07	0.07
3 – 4	0.54	0.53	0.52	0.53
4 – 5	0.68	0.66	0.65	0.66
5 – 6	0.63	0.65	0.66	0.65
6 – 7	0.66	0.64	0.64	0.64
7 – 8	0.64	0.65	0.65	0.65
8 – 9	0.65	0.65	0.65	0.65
9 – 10	0.65	0.65	0.65	0.65
10 – 11	0.65	0.65	0.65	0.65
11 – 12	0.65	0.65	0.65	0.65
12 – 13	0.65	0.65	0.65	0.65
13 – 14	0.65	0.65	0.65	0.65
14 – 15	0.65	0.65	0.65	0.65
15 – 16	0.65	0.65	0.65	0.65
16 – 17	0.65	0.65	0.66	0.65
17 – 18	0.65	0.65	0.66	0.65
18 – 19	0.65	0.65	0.66	0.65
19 – 20	0.65	0.65	0.66	0.65
Regression slope with simulation	0.9978[a]	1.0000	0.9953[a]	
R^2 of regression with simulation	0.9985	1.0000	0.9993	
MAE	0.0040	0.0000	0.0035	

[a] Regression slopes marked were found to be significantly different to 1, using a 2-sided Student's t-test ($p<0.05$), suggesting evidence for bias.

Table 3.3 Predicted annual calving rates across age classes for UK dairy cattle. Linear regressions were used to compare results from each model to the actual values from the test dataset. The regression slope and R^2 results of each analysis are presented alongside the mean absolute error (MAE) when comparing the model and actual results. In all regressions there were no significant intercept effects.

	Annual Calving Rate				
Age Class (years)	Model 1	Model 2	Model 3	Simulation	Actual
0 – 1	0.00	0.00	0.00	0.00	0.00
1 – 2	0.14	0.14	0.14	0.14	0.10
2 – 3	0.92	0.90	0.88	0.90	0.90
3 – 4	0.96	0.89	0.95	0.89	0.91
4 – 5	0.96	0.88	0.94	0.88	0.90
5 – 6	0.95	0.88	0.94	0.88	0.89
6 – 7	0.84	0.84	0.92	0.84	0.83
7 – 8	0.21	0.44	0.23	0.44	0.38
8 – 9	0.02	0.04	0.00	0.04	0.07
9 – 10	0.00	0.00	0.00	0.00	0.01
Regression slope with actual	0.9177[a]	1.0100[a]	0.9174[a]	1.0100[a]	
R^2 of regression with actual	0.9784	0.9951	0.9785	0.9951	
MAE	0.0470	0.0200	0.0510	0.0200	

[a] Regression slopes marked were found to be significantly different to 1, using a 2-sided Student's t-test ($p<0.05$), suggesting evidence for bias.

Table 3.4 Predicted annual calving rates across age classes for UK dairy cattle in seasonally calving herds. Linear regressions were used to compare results from each model to the actual values from the test dataset. The regression slope and R^2 results of each analysis are presented alongside the mean absolute error (MAE) when comparing the model and actual results. In all regressions there were no significant intercept effects.

	Annual Calving Rate				
Age Class (years)	Model1	Model2	Model3	Simulation	Actual
0 – 1	0.00	0.00	0.00	0.00	0.00
1 – 2	0.17	0.17	0.18	0.18	0.18
2 – 3	0.88	0.85	0.85	0.86	0.84
3 – 4	0.97	0.90	0.96	0.91	0.90
4 – 5	0.96	0.90	0.96	0.91	0.92
5 – 6	0.96	0.90	0.96	0.90	0.90
6 – 7	0.81	0.83	0.91	0.82	0.81
7 – 8	0.22	0.41	0.19	0.38	0.33
8 – 9	0.02	0.04	0.00	0.03	0.07
9 – 10	0.00	0.00	0.00	0.00	0.01
Regression slope with actual	0.9128[a]	0.9890[a]	0.8925[a]	0.9820[a]	
R^2 of regression with actual	0.9906	0.9940	0.9840	0.9968	
MAE	0.0390	0.0180	0.0490	0.0150	

[a] Regression slopes marked were found to be significantly different to 1, using a 2-sided Student's t-test ($p<0.05$), suggesting evidence for bias.

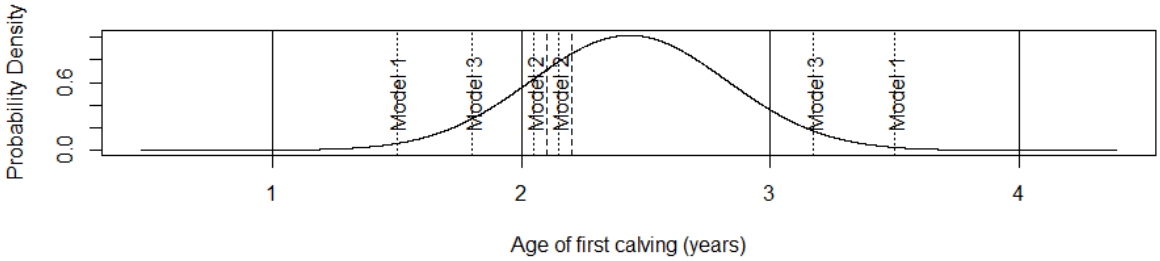


Figure 3.1. An illustration of the differences between Models 1-3. The graph shows the probability density of calving ages for a given parity, assuming that they are normally distributed with a mean of 2.4 years and a standard deviation of 0.4 years. In order to implement all three models, for each parity, an estimate of the mean age of calving within each age class is needed (examples of these estimates are marked on the diagram with vertical dotted lines with labels to indicate with model they are from).

In Model 1, each age class spans 1 year (boundaries marked with solid vertical lines) and the mean age of calving was simply estimated to be equal to the mid-point of the age class (as shown on the diagram for age classes 1-2 and 3-4 years). However, particularly for the non-modal age class, this is estimate is not accurate. Therefore, Models 2 and 3 used different methods to reduce the size of errors caused by this estimation.

Model 2 reduced the age class size from 1 to 0.1 years (boundaries marked by vertical dashed lines) and again uses the mid-point of the age class as an estimate of the mean (as shown on the diagram for the first two classes, 2.0-2.1 and 2.1-2.2 years, within 2-3 years). However as the size of the classes has been reduced, the difference between the mid-point and the true mean calving age for each age class is also reduced.

In Model 3, each age class again spans 1 year (boundaries marked by solid vertical lines) and characteristics of a normal distribution were used to calculate an approximate value for the mean calving age for each age class (as shown on the diagram for age classes 1-2 and 3-4 years).

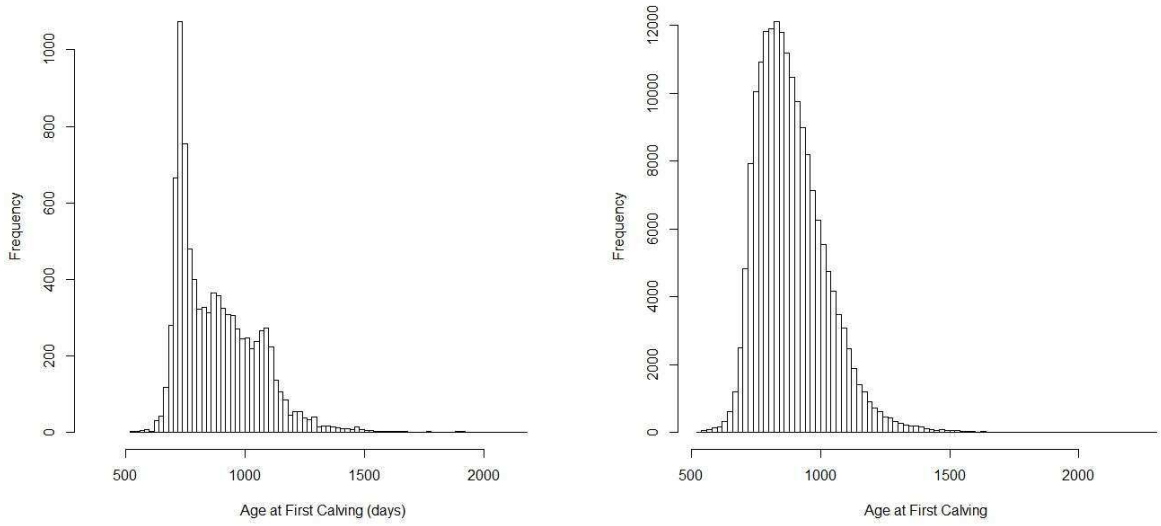


Figure 3.2 Distribution of observed age at first calving of cattle in seasonal calving herds (left) compared that of cattle in all herds (right) in our UK dairy population.

3.3 Chapter conclusion

Results show that models developed are effective at predicting age-specific calving rates from AFC and CI. As model 2, which reduced estimation errors by reducing the size of age class considered, performed best and the increased computation needed was not too large, this model was used for the remainder of the thesis.

Using Dickerson's genetic model (see Chapter 1), AFC and CI were predicted for a range of crossbred types for a case study of Boran x Holstein cattle in Ethiopia, described in Chapter 4 (Table 3.5). These values are used as inputs for model 2 developed in this chapter, along with values for standard deviations for AFC (282 days) and CI (146 days) which were reported by Demeke et al. (2004) from for the same case study system. Results are shown in Table 3.6 and used in Chapter 4 to predict herd composition for the case study under varying

crossing strategies. The same method could be used when modelling other systems, given genetic parameters for CI and AFC are available.

Table 3.5 Predicted age at first calving (AFC) and calving interval (CI) for a range of crossbred types in Ethiopian Boran x Holstein case study, described in Chapter 4. For definitions of crossbred types 1-18, see Chapter 4 and figure 4.1. Genetic additive and non-additive parameters (L, E, H and R) are for Boran are from long-term crossbreeding studies of Boran and Holstein cattle in Ethiopia (Birhanu et al., 2015). Weights (al, ae, h and r) are dependent on crossbred ancestry and the calculation of these is described in section 4.2.2.

Trait	L	E	H	R		
CI (days)	476.48	531.49	-70.14	-17.34		
AFC (days)	1388.11	1773.41	-354.47	-62.6		
Crossbred type ID	al	ae	h	r	AFC (days)	CI (days)
1	1	0	0	0	1388	476
2	0.5	0.5	1	0	1226	434
3	0.75	0.25	0.5	0.25	1292	451
4	0.75	0.25	0.5	0.25	1292	451
5	0.25	0.75	0.5	0.25	1484	478
6	0.5	0.5	0.5	0.5	1372	460
7	0.875	0.125	0.25	0.1875	1336	463
8	0.375	0.625	0.75	0.1875	1351	455
9	0.625	0.375	0.5	0.4375	1328	454
10	0.875	0.125	0.25	0.1875	1336	463
11	0.375	0.625	0.75	0.1875	1351	455
12	0.625	0.375	0.5	0.4375	1328	454
13	0.625	0.375	0.75	0.1875	1255	441
14	0.125	0.875	0.25	0.1875	1625	504
15	0.375	0.625	0.5	0.4375	1424	468
16	0.75	0.25	0.5	0.25	1292	451
17	0.25	0.75	0.5	0.25	1484	478
18	0.5	0.5	0.5	0.5	1372	460

Crossbred type	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Age class (years)																		
0 - 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
1 - 2	0.01	0.04	0.02	0.02	0.00	0.01	0.02	0.01	0.02	0.02	0.01	0.02	0.03	0.00	0.01	0.02	0.00	0.01
2 - 3	0.15	0.33	0.25	0.25	0.08	0.16	0.20	0.18	0.21	0.20	0.18	0.21	0.29	0.03	0.12	0.25	0.08	0.16
3 - 4	0.57	0.76	0.68	0.68	0.45	0.59	0.63	0.62	0.65	0.63	0.62	0.65	0.73	0.27	0.53	0.68	0.45	0.59
4 - 5	0.78	0.85	0.82	0.82	0.76	0.81	0.80	0.82	0.82	0.80	0.82	0.82	0.84	0.67	0.79	0.82	0.76	0.81
5 - 6	0.77	0.85	0.82	0.82	0.77	0.80	0.79	0.81	0.81	0.79	0.81	0.81	0.83	0.73	0.79	0.82	0.77	0.80
6 - 7	0.77	0.85	0.82	0.82	0.77	0.80	0.80	0.81	0.81	0.80	0.81	0.81	0.84	0.73	0.79	0.82	0.77	0.80
7 - 8	0.77	0.85	0.82	0.82	0.77	0.80	0.80	0.81	0.81	0.80	0.81	0.81	0.84	0.73	0.79	0.82	0.77	0.80
8 - 9	0.77	0.85	0.82	0.82	0.77	0.80	0.80	0.81	0.81	0.80	0.81	0.81	0.84	0.73	0.79	0.82	0.77	0.80
9 - 10	0.77	0.85	0.82	0.82	0.77	0.80	0.80	0.81	0.81	0.80	0.81	0.81	0.84	0.73	0.79	0.82	0.77	0.80
10 - 11	0.77	0.85	0.82	0.82	0.77	0.80	0.80	0.81	0.81	0.80	0.81	0.81	0.84	0.73	0.79	0.82	0.77	0.80
11 - 12	0.77	0.85	0.82	0.82	0.77	0.80	0.80	0.81	0.81	0.80	0.81	0.81	0.84	0.73	0.79	0.82	0.77	0.80
12 - 13	0.77	0.85	0.82	0.82	0.77	0.80	0.80	0.81	0.81	0.80	0.81	0.81	0.84	0.73	0.79	0.82	0.77	0.80
13 - 14	0.77	0.85	0.82	0.82	0.77	0.80	0.80	0.81	0.81	0.80	0.81	0.81	0.84	0.73	0.79	0.82	0.77	0.80
14 - 15	0.77	0.85	0.82	0.82	0.77	0.80	0.80	0.81	0.81	0.80	0.81	0.81	0.84	0.73	0.79	0.82	0.77	0.80
15 - 16	0.77	0.85	0.82	0.82	0.77	0.80	0.80	0.81	0.81	0.80	0.81	0.81	0.84	0.73	0.79	0.82	0.77	0.80
16 - 17	0.77	0.85	0.82	0.82	0.77	0.80	0.80	0.81	0.81	0.80	0.81	0.81	0.84	0.73	0.79	0.82	0.77	0.80
17 - 18	0.77	0.85	0.82	0.82	0.77	0.80	0.80	0.81	0.81	0.80	0.81	0.81	0.84	0.73	0.79	0.82	0.77	0.80
18 - 19	0.77	0.85	0.82	0.82	0.77	0.80	0.80	0.81	0.81	0.80	0.81	0.81	0.84	0.73	0.79	0.82	0.77	0.80
19 - 20	0.77	0.85	0.82	0.82	0.77	0.80	0.80	0.81	0.81	0.80	0.81	0.81	0.84	0.73	0.79	0.82	0.77	0.80

Table 3.6 Predicted age-specific calving rates for crossbred types 1-18 of the Ethiopian Boran x Holstein case study, described in Chapter 4. Values are predicted using the fertility model 2 and are defined as the probability a cow of a specific crossbred type gives birth within the specific age class.

Chapter 4: Crossbreeding cattle in sub-Saharan Africa: Modelling herd composition and performance under varying strategies

4.1 Introduction

Cattle are important in supporting development in Sub Saharan Africa (SSA) as they are a source of both food and income. However, studies show there is a substantial gap between the potential and realised production levels for livestock farming in this region due to shortfalls in management but also choice of appropriate animal genotypes (Henderson et al., 2016). The lack of consistent recording systems for both pedigree and performance data (Chagunda et al., 2015a) makes selective breeding difficult. Crossbreeding strategies require comparatively little data, are generally easy strategies to follow and results can be achieved more quickly, so are a good fit in SSA systems (Cunningham and Syrstad, 1987; Rutledge, 2001; Leroy et al., 2015).

Crossbreeding allows farmers to take advantage of the complementary fitness traits from local breeds and production traits from exotics, as well as providing favourable heterosis. A variety of crossbreeding strategies can be used in systems in SSA. Firstly, a single sire type can be used over multiple generations to grade up from a local breed to a higher proportion of exotic genes, for example to a high level of exotic by using a purebred exotic bull, or to 50% by using a crossbred bull sired by an exotic, out of a local cow (F1). Although these strategies allow farmers to take advantage of traits from other breeds, the benefit of heterosis reduces across generation. To maintain high levels of heterosis, rotational crossbreeding strategies can be used where multiple purebred sire types are used over years or generations, maintaining higher levels of heterosis compared to grading up strategies (Cunningham and Syrstad, 1987).

When deciding which system is most suitable we need a model to predict how herds will perform over time under these varying strategies (Amer et al., 2003). The purpose of the present study was to produce such a model for crossbreeding in SSA systems, thereby also addressing the third and fourth objectives of the thesis. In order to do this, we combine two models: firstly, a deterministic herd model to simulate the changing herd breed composition over time, depending on the crossbreeding strategy; secondly, a genetic model to predict the performance of each possible cross type for a given trait, given the additive and non-additive genetic effects for the pair of breeds and trait of interest.

In the present study, we illustrate the use of this model by simulating crossbreeding between Boran and Holstein cattle. Boran is a zebu breed which originates from Kenya and Ethiopia. It is common for dairy farmers in these countries to use imported Holstein semen on their Boran cows to produce more animals with higher milk yields, so this is a relevant system in which to test the model, although it could also be used to test crossing strategies for any pair of breeds. We assume the initial herd is purebred Boran. Sires that can be used are purebred Boran, purebred Holstein or an F1 bull sired by a Holstein as these options are all likely to be practical either by using artificial insemination (AI) or a locally-bred bull.

We considered the effect of varying crossing strategies on the herd performance for two traits. Firstly, we considered annual milk yield, expressed as an average across all cows in the herd. This trait is of particular interest because increasing the amount of milk produced means greater availability of both food and a product to sell to increase income. Secondly, we considered average yearling weight. This trait has an important impact on the profitability of a farm as heavier yearlings will have greater feed costs and smallholder farmers in SSA are known to prefer smaller, more efficient cows (Chawala et al., 2019).

4.2 Materials and methods

Our models were designed to predict the effect of varying crossbreeding strategies on an initial purebred herd of a local breed. Sires used could be the local low-input and low-output breed an exotic high-producing breed or an F1 cross between the two breeds. A single type of sire could be used across all types of females, or specific sire types could be used for specific female types, for each year across the timescale modelled, which in our case was 40 years.

We tested 5 strategies (see Table 4.1). We considered two strategies where a single sire type was used on all females for the full duration of the study: either an exotic or F1 sire. We considered two strategies where sires used were rotated across years: a balanced rotation where the sire type was alternated between exotic and local breeds every year, and an unbalanced rotation where an exotic sire was used for 3 years, followed by a local sire for a single year, with this pattern then repeated. Finally, we considered a true rotation strategy where the sire used on a given female depended on the ancestry of that female. Cows sired by a local sire were mated to an exotic breed, whereas cows sired by an exotic breed were mated to a local sire breed, meaning that the sire breed used rotated every generation rather than every year.

Table 4.1. Crossbreeding strategies. The table shows the 5 crossing strategies tested and the sire types used each year: Exotic (E), Local (L) or F1. After year 4, the same pattern is repeated for the full timescale modelled (here 40 years).

Strategy		Year 1	Year 2	Year 3	Year 4
1. Exotic		E	E	E	E
2. F1		F1	F1	F1	F1
3. Balanced rotation		E	L	E	L
4. Unbalanced rotation		E	E	E	L
5. Specific sire	Cows with local sire	E	E	E	E
	Cows with exotic sire	L	L	L	L

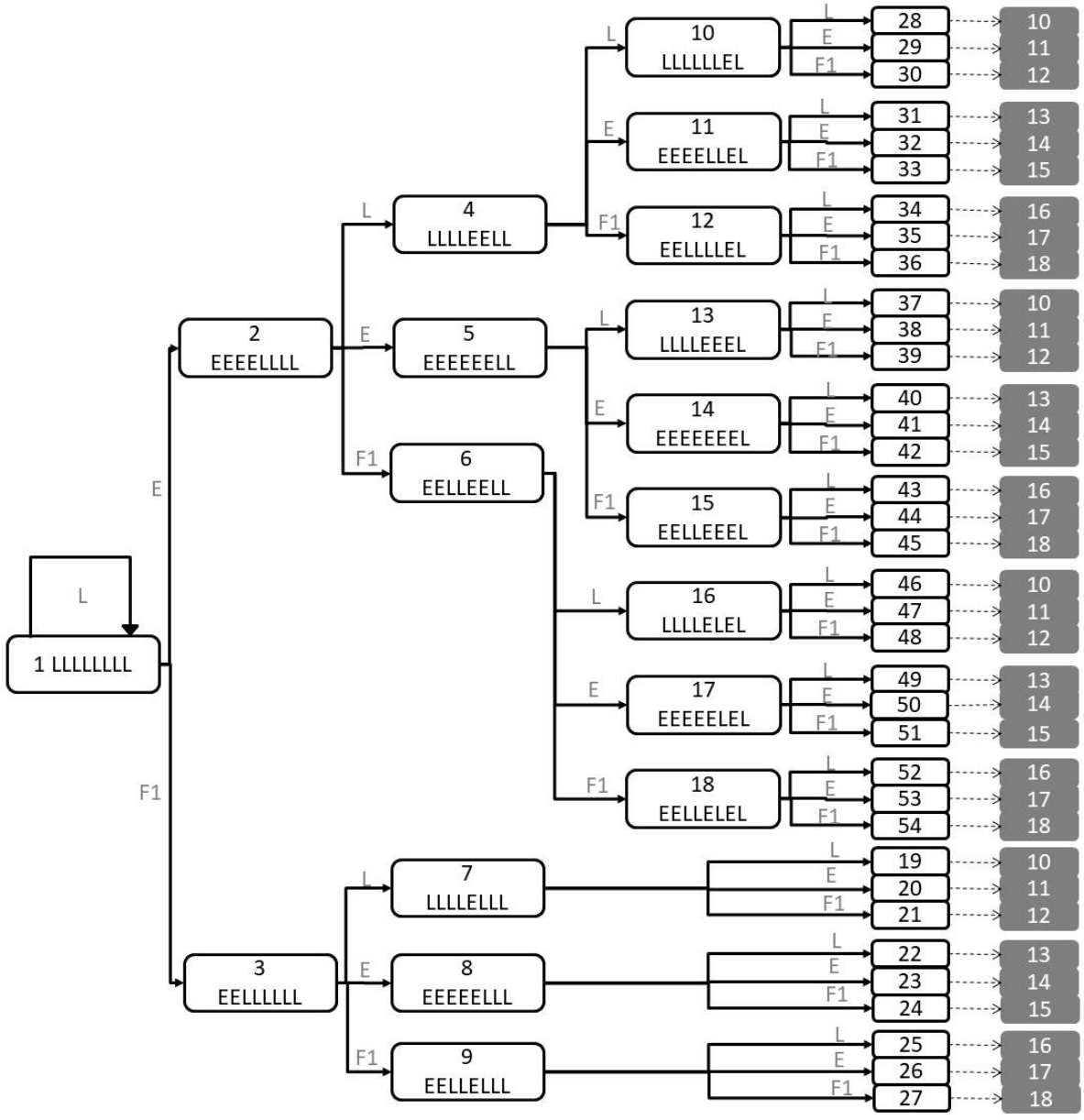
4.2.1 Herd Composition Model

The aim of this deterministic model is to predict how varying the cross breeding strategy affects the herd composition over the timescale modelled (40 years). We defined herd composition as $\propto_{i,j,k}$, which is equal to the number of individuals in the herd in year i, of cross type j and age k (1-20 years).

We defined 18 possible cross types which are different types of pure or crossbred animals with varying pedigrees. Figure 4.1 shows cross types that can be produced by beginning with a purebred local individual and using any of the three sire types: local (L), exotic (E) or F1. Cross types were given IDs made up of 8 characters, each of which represents the breed (L or E) of the 8 great grandparents in the order of: paternal grandfather's sire, paternal grandfather's dam, paternal grandmother's sire, paternal grandmother's dam, maternal grandfather's sire, maternal grandfather's dam, maternal grandmother's sire and maternal grandmother's dam. Cross types 1-18 can be described using this naming scheme as all 8 of

the great grandparents are purebred L or E. With each new generation there were exponentially more cross types so we limited the model to cross types 1-18. Cross types 19-54 have one or more great grandparents that are not purebred L or E and were allocated back into cross types 10-18 depending on their breed composition as shown in Figure 4.1.

Figure 4.1. Possible cross types produced, starting with purebred local animal (LLLLLLLL) and using a purebred local (L), purebred exotic (E) or an F1 sired by an exotic (F1) as sires. Offspring of cross types 7-18 (cross types 19-54) are allocated to a cross types 10-18, according to which they are most similar to.



The model uses survival rates to simulate the number of animals within each age class (1 year from birthday to birthday, 20 classes starting at age 1 year) for each cross type (1-18) for each year (0-40). The total number of cows calving per cross type per year was then calculated using the number of animals in each age class and age class and cross type specific calving rates.

The cross type of calves produced by calving cows was determined by the sire used on the cow cross type in that year, which varied according to breeding scenario. Total number of calves born of each cross type per year was calculated, assuming that no twins are born. This number was multiplied by a cross type specific replacement rate which is a function of the survival and calving rate and is equal to the proportion of calves that must be kept as replacements in order to keep the herd at a constant number of cows (irrespective of calving rate). Here we assumed that there was no selection among potential replacement females and cross types are kept in the proportion in which they are born. This gives the number of yearlings for each cross type in the following year.

For animals greater than 1 year old, when k> 1, herd composition, $\propto_{i,j,k}$, is calculated as:

$$\propto_{i,j,k} = \propto_{i-k+1,j,k=1} s_{j,k}$$

where, $s_{j,k}$ is equal to the probability that an animal of cross type j will survive until age k.

In order to model the initial herd, when i<1 and k = 1, $\propto_{i,j,k}$, is calculated as:

$$\propto_{i,j,k} = \mathrm{K}_j \left(\sum_k s_{j,k} \right)^{-1}$$

where K_j is the number of animals of cross type j in the initial herd.

In subsequent years (when i ≥ 1), the number of yearling heifers (k=1), $\propto_{i,j,k=1}$ is calculated as:

$$\propto_{i,j,k} = \eta_{i-1,j}^{m=R}$$

where $\eta_{i,j}^{m=m}$ is the number of animals in year i, or cross type j in class m, where m is equal to C for cows calving, R for replacement females being reared or B for all calves born.

The number of replacements (m=R) in year i of cross type j is calculated as follows:

$$\eta_{i,j}^{m=R} = \eta_{i,j}^{m=B} \rho_j$$

where ρ_j is the proportion of all calves of cross j born (dead or alive) that are kept as replacements in order to maintain a herd of cross j at a constant size and is calculated as follows:

$$\rho_j = \left(\sum_k [s_{j,k} c_{j,k}] \right)^{-1}$$

where $c_{j,k}$ is equal to a probability of a cow of cross type j calving at age k.

The number of calves born (dead or alive) (m=B) in year i and off cross type j, is calculated as follows:

$$\eta_{i,j}^{m=B} = \sum_l \sum_{j\prime} [x_{j,j',l} m_{i,j',l} \eta_{i,j\prime}^{m=C}]$$

where x is a matrix that is used to determine the cross type of offspring and $x_{j,j',l}$ takes a value of 1 if sire l (l = L, E or F1) mated to a dam of cross j' generates an offspring of cross k. Otherwise, it takes a value of 0. Values of this matrix can be found using the pedigree structure shown in figure 4.1.

m is a matrix used to define the sire type used and $m_{i,j',l}$ is equal to the proportion of dams of cross j', calving in year i that were mated to a sire type l. This matrix varies depending on the crossing strategy being tested and under all scenarios tested here, values are equal to 0 or 1.

The number of cows calving (m=C) in year i and off cross type j, is calculated as follows:

$$\eta_{i,j}^{m=C} = \sum_k (\alpha_{i,j,k} c_{j,k})$$

4.2.2 Genetic model

The performance for a trait for a specific cross type was predicted using a genetic model of additive and non-additive breed effects. A number of models for non-additive effects have been proposed that vary in the way they model epistasis (whether interactions are between or within additive and dominance effects) (Dickerson, 1969, 1973; Kinghorn, 1980; Grosshans et al., 1994; Wolf et al., 1995; Kahi et al., 2000b). When tested using data from a crossbreeding study in Ethiopia, the Dickerson (1973) model performed the best (Demeke et al., 2003a) and had the added benefit of being less complex than other models.

Dickerson's model (Dickerson, 1973) which includes additive, heterosis and recombination loss effects was used to predict animal cross performance. The mean performance for a trait of an individual of cross type j can be estimated:

$$Performance_{j,trait} = al_j L_{trait} + ae_j E_{trait} + h_j H_{trait} + r_j R_{trait}$$

al, ae, h and r are weights which characterise the proportion of the additive effect for the local breed, the additive effect of the exotic breed, the heterosis, and the recombination loss, respectively, as expressed by an individual of cross type j; al and ae are simply equal to the proportion of local and exotic ancestry in cross type j; h is the proportion of the maximum heterosis (expressed by an F1) which pertains to the cross type j. The value of h was calculated as the following:

$$h_j = al_{sire} ae_{dam} + al_{dam} ae_{sire}$$

where al_{sire}, al_{dam}, ae_{sire}, ae_{dam} are the proportion of local ancestry in the sire and dam of cross type j and exotic ancestry in the sire and dam of cross type j.

In model (1), r is a measure of the average amount of recombination that has occurred between parental haplotypes. This is the mean fraction of independently segregating pairs of loci in gametes from both parents that are expected to be different from that found in either purebred and r_j was calculated as the following:

$$r_j = al_{sire}ae_{sire} + al_{dam}ae_{dam}$$

L and E are the mean performance for a trait of purebred local and exotic individuals, respectively. H is the maximum heterosis expressed by F1 crossbreds of this pair of breeds for the trait. R is the theoretical recombination loss expressed for the trait for crossbreds of this pair of breeds if r were equal to 1. Values for L, E, H and R are specific to a given trait, pair of breeds and environment or system. These values are obtained from published data, where they have been estimated using long-term crossbreeding studies which measure the performance of a range of crossbred individuals.

Finally, the results of the two models were combined to predict herd performance for the trait over time. For each year, the number of individuals that expressed the trait of each cross type (from the herd model), $\eta_{i,j}^{m}$, was multiplied by the predicted performance of that cross type for the trait (from the genetic model), $Performance_{j,trait}$. These were then totalled across cross types within each year expressed per animal, as follows:

$$Trait_i = \frac{\sum_j \eta_{i,j}^{m}.Performance_{j,trait}}{\eta_{i,j}^{m\prime}}$$

where both m and m' are specific to the trait being estimated, m is the class of animals that express the trait and m' is the class of all animals that could express the trait. These can be the same class, for example, for yearling weight, both are replacement heifers. Alternatively they can be different classes, for example, for milk yield, m is all cows that calve and

therefore begin a lactation, whereas m' is all adult (k>1) cows in the herd, including dry cows.

4.2.3 Case study: Boran x Holstein in Ethiopia

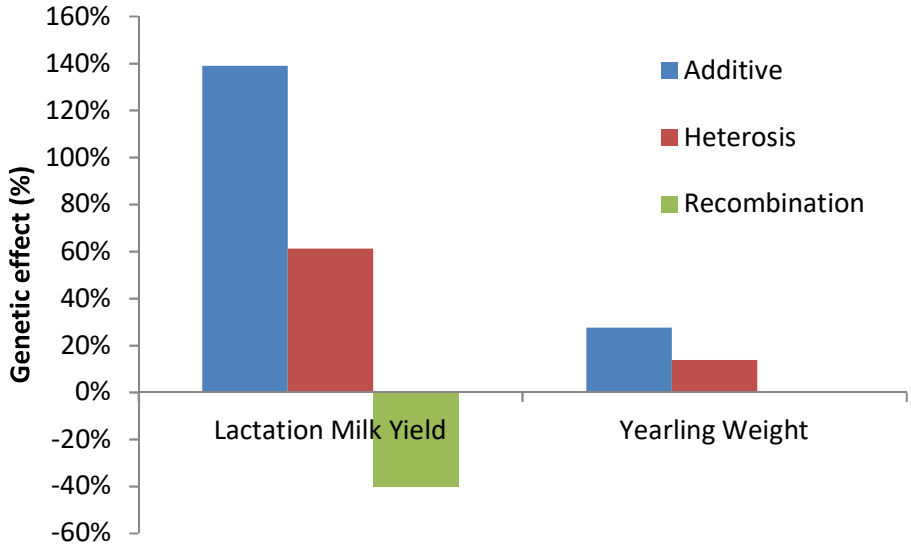
To test the models, a case study of crossbreeding Boran and Holstein cattle in Ethiopia was used. Boran was the local and Holstein the exotic breed. A value of 0.76 was used for the annual survival rate, as a survey of cattle herd dynamics in the Oromia region of Ethiopia found that the average annual death rate was 24% (Asfaw and Jabbar, 2008). This value was used for all cross types (j) to calculate $s_{j,k}$. To estimate age specific calving rates for each cross type, $c_{j,k}$, a genetic model (Dickerson, 1973) and additive and non-additive genetic parameters from long-term crossbreeding studies of Boran and Holstein cattle in Ethiopia (Birhanu et al., 2015) were used to estimate the age at first calving and calving interval for each cross type, which were then used as inputs in a deterministic model, as described in Chapter 3.

The traits we chose to examine were lactation milk yield and yearling weight, as they differ in the timing and continuity of their expression. Lactation milk yield is of interest as it is a production trait and, therefore, directly linked to farmer income, and impacts of breeding decisions extend over the entire productive life of the cow. Yearling weight is linked to rearing costs and young animals mature through the system relatively quickly, and so traits expressed by young animals have a more transient impact on the herd. Results for milk yield have been expressed here as annual milk yield per cow in the herd, whereas results for yearling weight have been expressed as average yearling weight per yearling in the herd. The additive and non-additive genetic parameters for both traits came from Ethiopian

crossbreeding studies of Boran and Holstein cattle milk yield (Birhanu et al., 2015) and yearling weight (Haile et al., 2011).

The largest genetic effect for both traits was the additive effect, with Holstein cattle both producing more milk and weighing more as yearlings. When scaled, by considering values as percentages of the average of the two purebreds, we see that the size of all genetic effects for lactation milk yield were greater than those for yearling weight (see Figure 4.2). A significant effect of recombination loss was modelled for lactation milk yield, but not for yearling weight, as studies of these breeds in Ethiopia have not estimated a recombination effect.

Figure 4.2. A chart comparing the size of the additive and non-additive genetic effects, expressed as a percentage of the average performance of the two purebred types, for lactation milk yield and yearling weight. The additive effect is equal to the difference in performance between purebred Holsteins and Borans. The heterosis effect is the maximum heterosis expressed by a crossbred, which is equal to the difference between the average of the two purebreds' performance and the F1 performance. The recombination effect is the theoretical recombination loss expressed for the trait for Boran x Holstein crossbreds if r were equal to 1. Values are from long-term crossbreeding studies of Boran and Holstein cattle in Ethiopia (milk yield (Birhanu et al., 2015) and yearling weight (Haile et al., 2011)).



A sensitivity analysis was carried out for the genetic effect parameters. The difference between L and E and the values for H and R were varied for both traits, considering a 10% increase or decrease in the size of each. All combinations of -10%, 0% or +10% change for each genetic effect were considered. The amount by which E was greater than L was also increased in small increments in order to find the threshold (to the nearest 1%) where the ranking of strategies changed. For yearling weight, where no recombination loss effect was included due to the Ethiopian study not reporting a significant effect (Haile et al., 2011), the

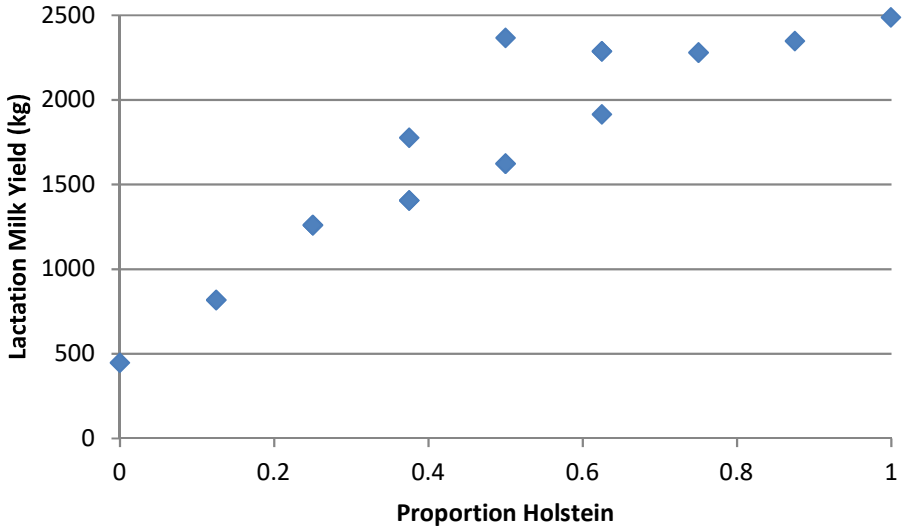
effect of including a non-zero value for R was also tested. Recombination loss is expected to be in the opposite direction as heterosis (Rutledge, 2001), so for yearling weight where heterosis for the trait is positive (see results of chapter 2), we expect the recombination loss effect to be negative. Therefore inclusion of varying magnitudes of negative recombination loss for yearling weights was also tested.

4.3 Results

4.3.1 Milk Yield

The results of the genetic model for lactation milk yield are shown in Figure 4.3. As expected, purebred Borans (0% Holstein) had the lowest milk yields and in general, higher proportion Holstein individuals produced more milk. However, F1 individuals had predicted lactation milk yields very close to that of purebred Holstein individuals due to the high levels of heterosis. It is worth noting that other individuals with 50% Holstein genetics that were not first crosses, had milk yields closer to the average of the two purebred types, as they express less heterosis and more recombination loss. Similarly, other cross types that were sired by a crossbred bull had lower milk yields than those with the same proportion of Holstein genetics but sired by a purebred bull. Due to the recombination effect for this trait, 75% Holstein individuals had predicted milk yields slightly lower than F1 individuals.

Figure 4.3. Predicted lactation milk yield for crossbred individuals with varying proportions of Holstein genetics. As shown, multiple types of crossbred with the same proportion of Holstein genetics can have varying predicted milk yields. This is due to varying expression of non-additive genetics effects, due to the proportion of Holstein genetics present in their parents. In particular, an F1 individual (parents with 0 and 100% Holstein genetics) and an F2 individual (parents both with 50% Holstein genetics), both have 50% Holstein genetics, but express different values of heterosis (F1: 1, F2:0.5) and recombination loss (F1:0, F2:0.5).



All five strategies tested increased the annual milk yield per cow compared to the initial level of 200 kg (Figure 4.4). The Holstein sire, unbalanced rotation and true rotation strategies all had the greatest initial rate of increase, whilst the F1 sire strategy led to the slowest rate of increase.

The Holstein sire strategy had one of the fastest rates of increase in milk yield initially and peaked at an annual milk yield of 929 kg per cow in year 11. However after this point, annual milk yields under this strategy dropped to 852 kg per cow in year 25 and then reduced slightly until reaching 832 kg per cow in year 40.

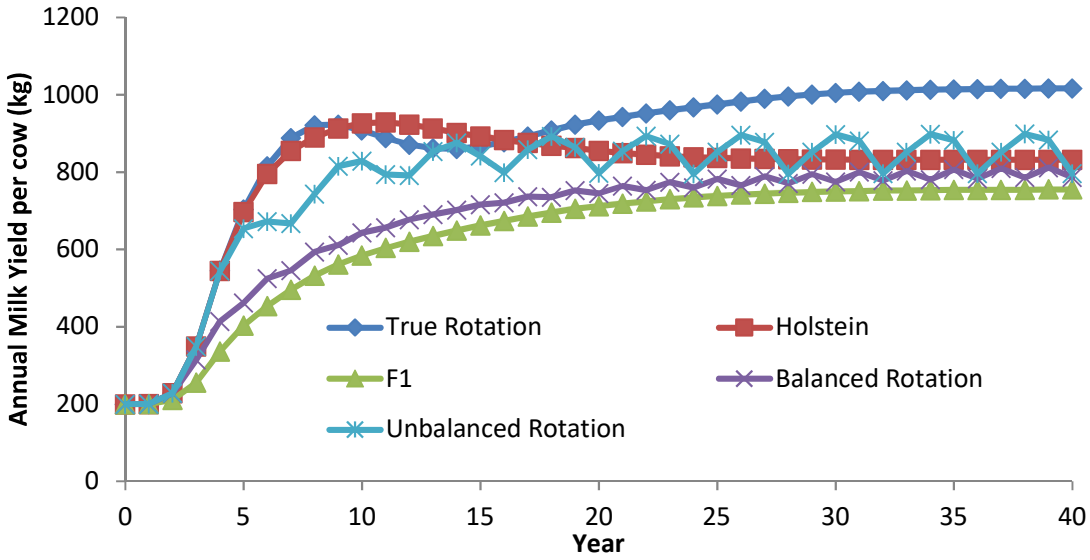
The F1 sire strategy had the lowest annual milk yield per cow of any strategy tested in every of the 40 years modelled, increasing slowly and levelling off, until reaching a maximum annual milk yield of 755 kg per cow by year 37.

The balanced rotation strategy performed just above the F1 strategy, despite annual milk yields fluctuating slightly each year, reaching annual milk yield of 812 kg and 797 kg per cow in years 39 and 40, respectively.

The unbalanced rotation strategy performed similarly to the Holstein sire strategy until year 5. From year 5 to 17, milk yields under this strategy were lower than the Holstein sire strategy, although higher than under either the F1 or balanced rotation strategies. From years 20-40, milk yields under this strategy were on average similar to those under the Holstein sire strategy. However the fluctuations in milk yield under this strategy were the greatest; for example, in year 38, milk yield was 899 kg per cow compared to 796 kg and 797 kg per cow in years 36 and 40 respectively.

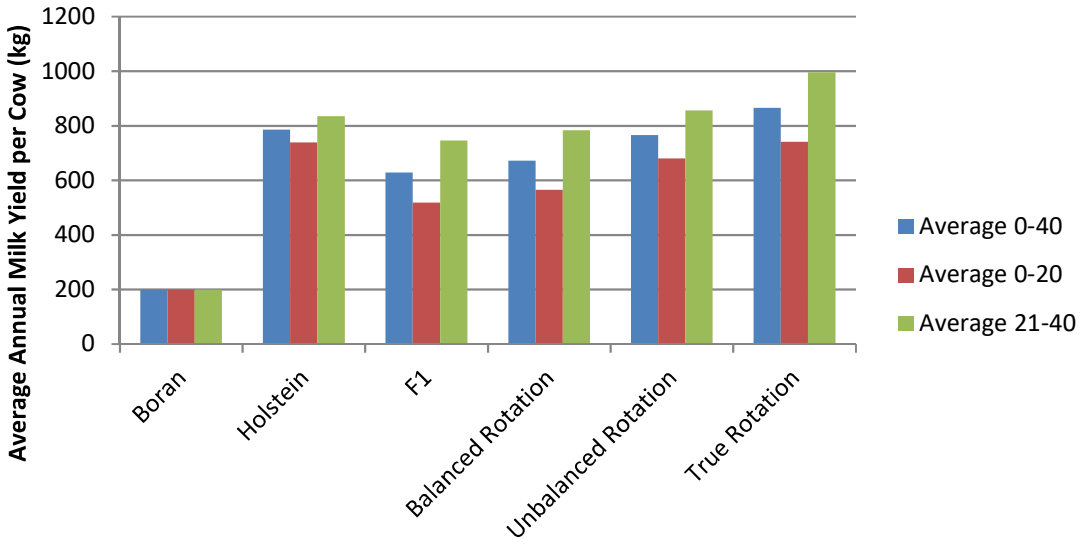
Again, annual milk yields for the true rotation strategy were similar to those for the Holstein sire strategy until year 5. From years 5-9, the true rotation strategy slightly outperformed the Holstein sire strategy, but after year 9, annual milk yields under this strategy reduced slightly until year 14, when they increased again. In year 17, the true rotation strategy again has the highest annual milk yield per cow for the rest of the time modelled, increasing slowly and levelling off at around year 36, eventually reaching 1017 kg in year 40.

Figure 4.4. Annual milk yield per cow across the 40 years modelled, under the 5 strategies tested (Holstein, F1, Balanced rotation, Unbalanced rotation and True rotation).



Whether we consider the whole 40 years modelled, the first 20 years or the last 20 years, the true rotation strategy results in the highest average annual milk yield per cow (865 kg over years 0-40) (Figure 4.5).

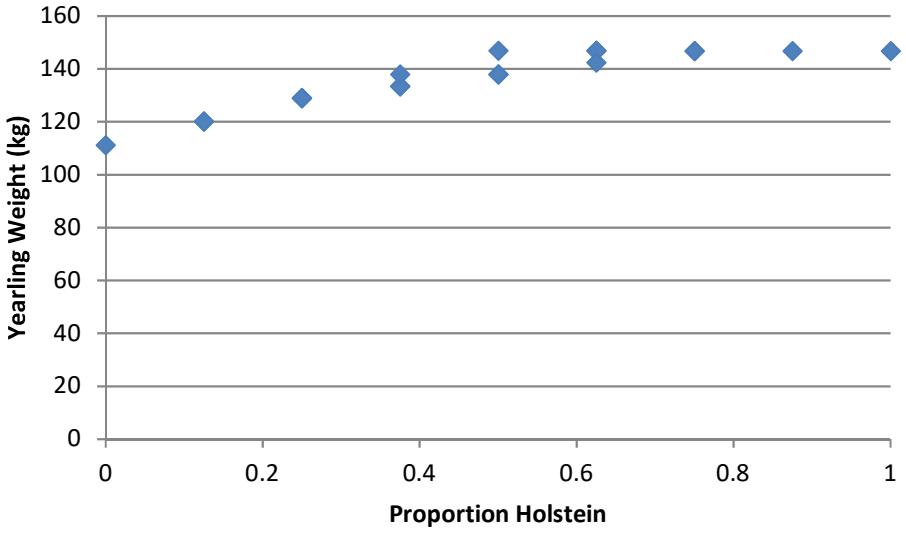
Figure 4.5. Average annual milk yields per cow for the five strategies tested (Holstein, F1, Balanced rotation, Unbalanced rotation, True rotation), compared to the baseline of purebred Boran, over different time periods (Years 0-40, Years 0-20 and Years 21-40).



4.3.2 Yearling Weight

Compared to milk yield, there was much less variation in the predicted yearling weight of different crossbred individuals (Figure 4.6). Yearling purebred Borans (0% Holstein) were predicted to weigh the least and F1s the most, although all individuals with more than 50% Holstein genetics were predicted to have similar weights. Cross types that were sired by a crossbred bull had lower yearling weights than those with the same proportion of Holstein genetics but sired by a purebred bull due to lower levels of heterosis.

Figure 4.6. Predicted yearling weights for crossbred individuals with varying proportions of Holstein genetics. As shown, multiple types of crossbred with the same proportion of Holstein genetics can have varying predicted yearling weights. This is due to varying expression of non-additive genetics effects, due to the proportion of Holstein genetics present in their parents. In particular, an F1 individual (parents with 0 and 100% Holstein genetics) and an F2 individual (parents both with 50% Holstein genetics), both have 50% Holstein genetics, but express different values of heterosis (F1: 1, F2:0.5).



As with the results for milk yield, all five strategies tested led to an increase in the average yearling weight compared to the initial value of 111 kg for purebred Borans (Figure 4.7). The

Holstein sire strategy led to the greatest rate and level of increase, with average yearling weight rising to 147 kg in year 1 and remaining approximately constant for the rest of the time period modelled.

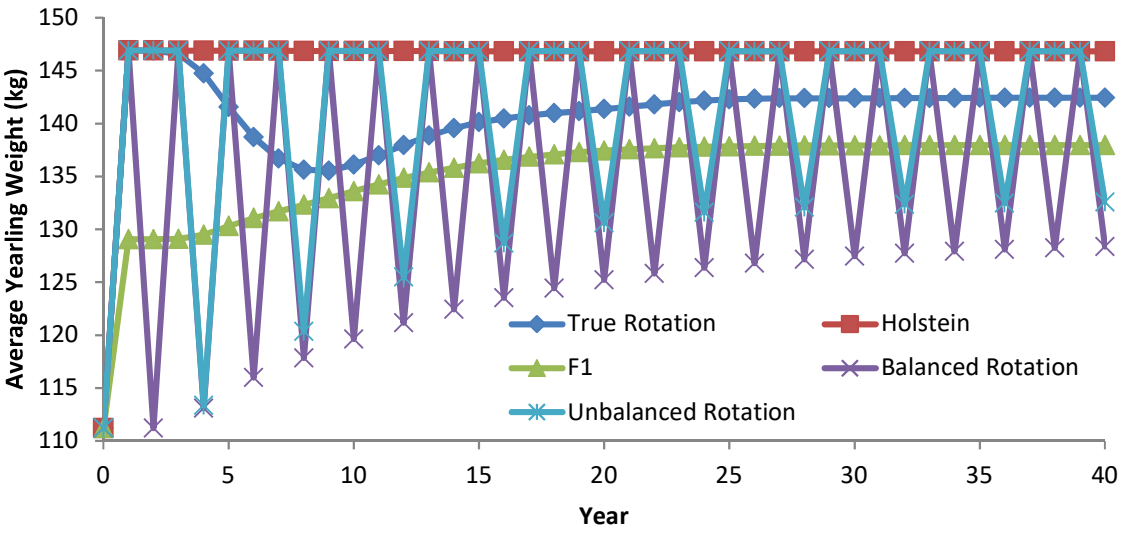
The F1 sire strategy led to a smaller increase in average yearling weight, with this rising to 129 kg in the first year, and then slowly increasing until levelling off at 138 kg after about 20 years.

Both the balanced and unbalanced rotation strategies led to fluctuating average yearling weights. Under the balanced rotation strategy, average yearling weight in year 1 was the same as under the Holstein sire strategy. However in year 2, this dropped to a similar level found in the purebred Boran herd. Average yearling weights under this strategy continued to oscillate each year, between those predicted under the Holstein strategy and a lower value. The size of these oscillations reduced over time so that average yearling weight under this strategy was 147 kg and 128 kg in years 39 and 40, respectively.

Under the unbalanced rotation strategy, average yearling weight followed that predicted under the Holstein sire strategy, except that every 4 years, starting in year 4, it dropped down to a lower level. The size of these drops decreased over time and was smaller than those found under the balanced rotation strategy, so that average yearling weights were 146 kg and 133 kg in years 37-39 and 40, respectively.

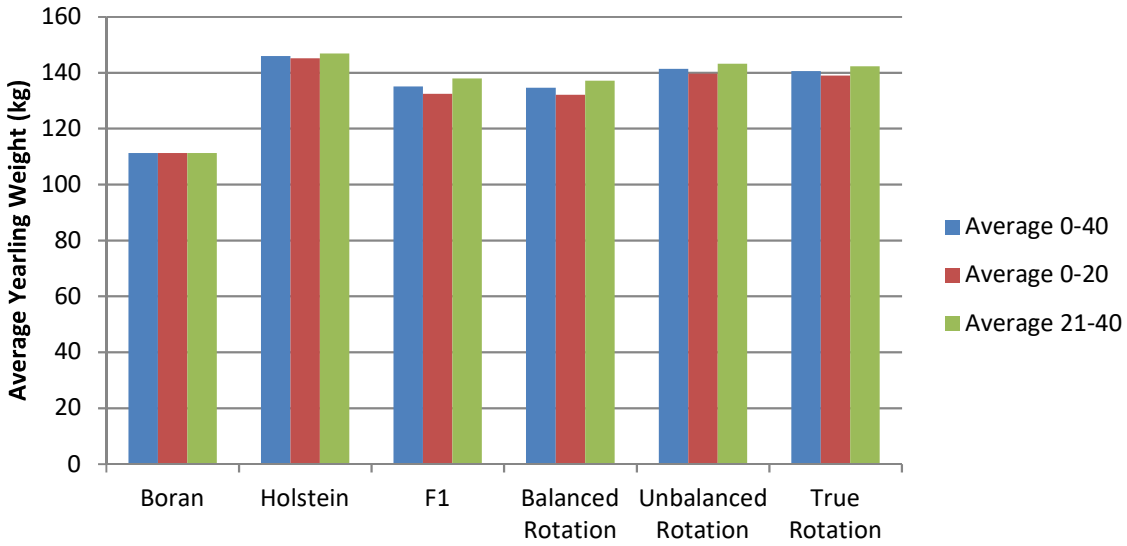
Under the true rotation strategy, average yearling weights for the first 3 years followed those predicted under the Holstein sire strategy. However from year 3-9, they dropped from 147 kg to 136 kg. After this, they rose again slowly but maintained a lower level than under the Holstein sire strategy, levelling off at 142 kg at about year 21.

Figure 4.7. Average yearling weight, measured in kg, across the 40 years modelled under the 5 strategies tested (Holstein, F1, Balanced rotation, Unbalanced rotation and True rotation).



Whether we considered the whole 40 years modelled, the first 20 years or the last 20 years, the Holstein sire consistently had the highest average yearling weights, with an average yearling weight of 146 kg over years 0-40 (Figure 4.8). The F1 sire and unbalanced rotation strategies had the same lowest average yearling weights over years 0-40 and years 0-20 of 135 kg and 132 kg, respectively. However when considering years 21-40, the F1 sire strategy had a slightly lower average yearling weight of 138 kg compared to 137 kg under the balanced rotation strategy.

Figure 4.8. Average yearling weights for the five strategies tested (Holstein, F1, Balanced rotation, Unbalanced rotation, True rotation), compared to the baseline of purebred Boran, averaged over different time periods (Years 0-40, Years 0-20 and Years 21-40).



Comparing results for the two traits, both traits showed increases under all strategies tested compared to the initial herd of purebred Boran. Strategies were broadly similarly ranked, with the Holstein and true rotation strategies tending to show greater levels of increase, whereas the balanced and F1 strategies tended to show lower levels of increase.

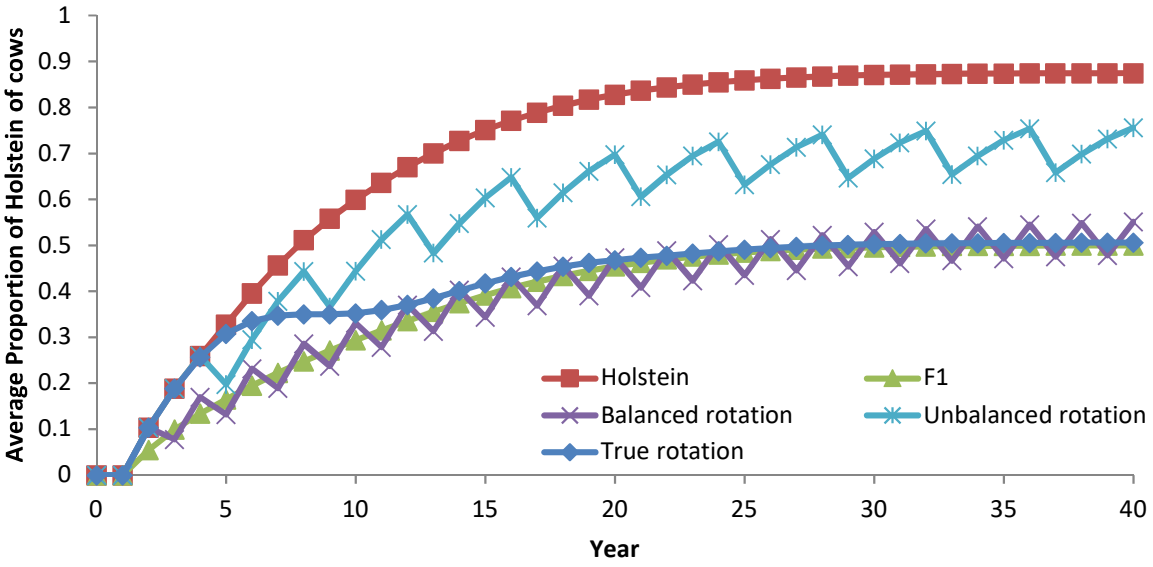
However, proportional changes in the traits due to the breeding strategies used were considerably greater for milk yield than yearling weight. The Holstein sire and true rotation strategies increased annual milk yields per cow up to a maximum of 4.7 and 5.1 times that of a herd of purebred Borans, respectively. For yearling weight, these same two strategies increased average yearling weight only up to a maximum of about 1.3 times that found in a herd of purebred Boran. This also meant that the variation in performance due to differing strategies was smaller for yearling weight than for milk yield.

Whilst being less sensitive to changes between strategies, changes in yearling weight tended to happen more quickly than changes in milk yield. The change from minimum to maximum yearling weight under the Holstein strategy occurred almost fully from year 0 to 1, whereas, under the same strategy, it took 11 years to reach the highest average milk yield.

4.3.3 Genetic effects in cows

All five strategies led to increased proportion of Holstein genes and expression of non-additive genetics effects compared to the initial herd of purebred Boran. Unsurprisingly, the Holstein sire strategy led to the greatest increase in proportion of Holstein genetics. Although note that due to limitations of the model, this never reaches 100% Holstein. The F1 sire, balanced rotation and true rotation strategies all only reached 50% Holstein genetics, although the true rotation strategy showed a greater initial rate of increase and the balanced rotation strategy showed yearly fluctuations, whilst following the pattern for the F1 sire strategy on average. The unbalanced rotation again showed fluctuations in the proportion of Holstein genetics, with a reduction once every 4 years. On average, this strategy resulted in an intermediate level of Holstein genetics, between that of the Holstein sire and other strategies (Figure 4.9).

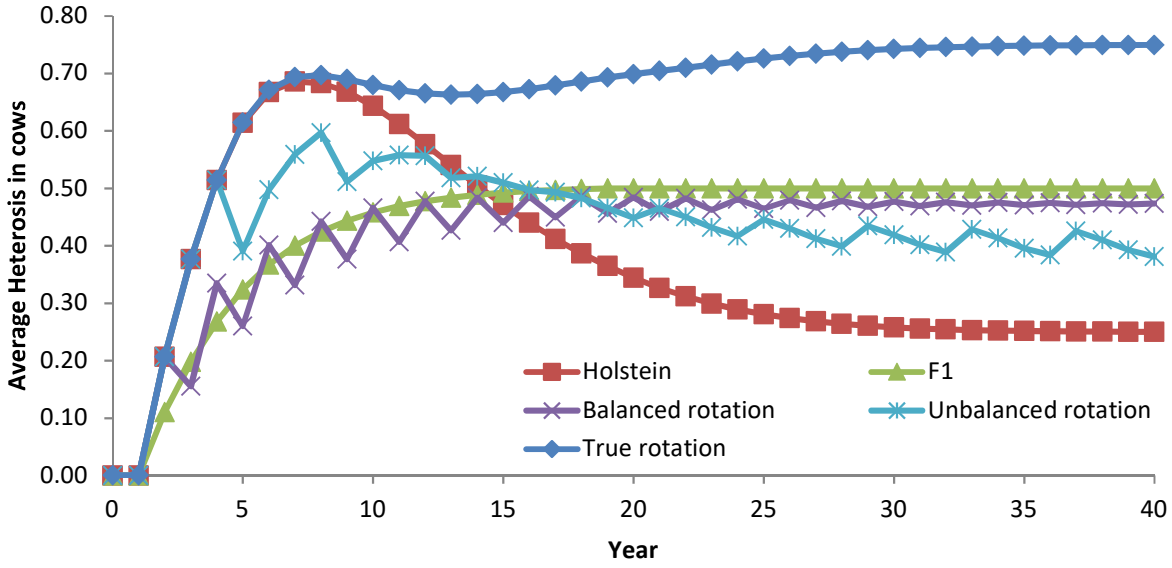
Figure 4.9. Average proportion of Holstein genetics in the adult cows (>1 years of age) in the herd under the five crossbreeding strategies tested and over the 40 years modelled.



The Holstein sire strategy led to a steep increase in the average heterosis in the cows of the herd from 0 up to 70% of the potential maximum, until year 8, when this reduced again, eventually levelling off and reaching 25% in year 40. The F1 sire strategy increased average cow heterosis up to 50% of the maximum by year 16 and this remained at this level for the rest of the period modelled. Average cow heterosis under the balanced rotation strategy fluctuated annually but, on average, followed that predicted under the F1 sire strategy. Under the unbalanced rotation strategy, for years 0-4, average cow heterosis followed that predicted under the Holstein sire strategy. However for years 4-13, it fluctuated and was lower than average cow heterosis under the Holstein sire strategy. For years 13-40, average cow heterosis under this strategy continued to fluctuate and on average reduce so that by year 40, it was lower than under the F1, but greater than under the Holstein sire strategy. Average cow heterosis under the true rotation strategy initially followed that of the Holstein sire strategy, until year 8, when rather than dropping significantly, there was a small

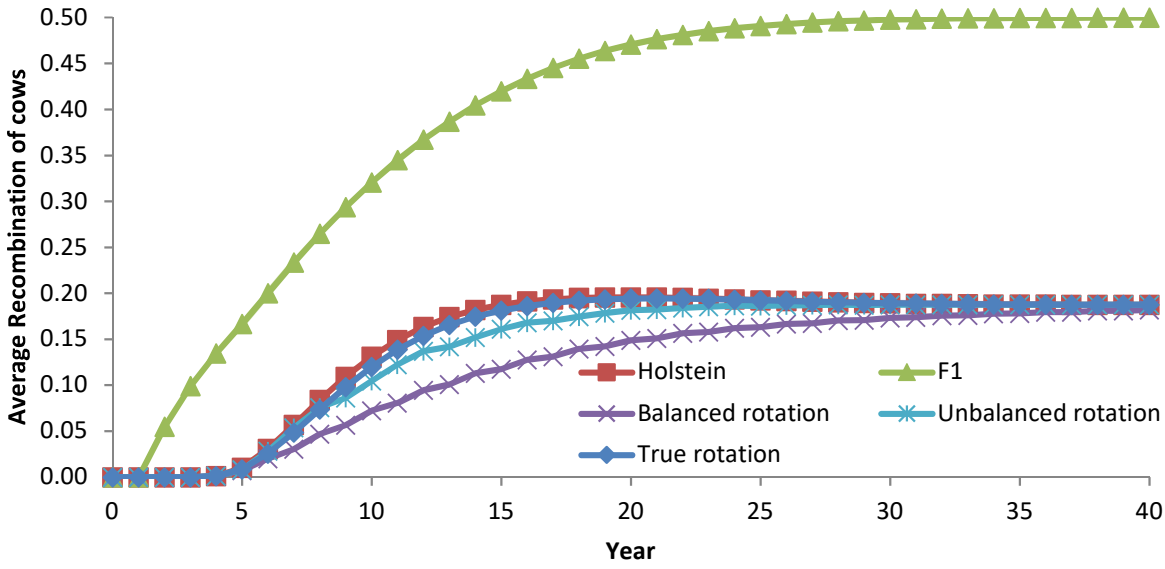
reduction in heterosis before it climbed slightly again from 66% in year 13 to 75% in year 40 (Figure 4.10).

Figure 4.10. Average heterosis of adult cows (>1 years of age) in the herd, under the five crossbreeding strategies tested and over the 40 years modelled.



The F1 sire strategy showed much greater levels of recombination compared to all other strategies tested, reaching the maximum of 0.5 after 28 years. Under all other strategies, recombination only reached a maximum of about 0.2. However, the rate of increase was lowest under the balanced rotation strategy, meaning it had the lowest levels on average over the 40 years modelled (Figure 4.11).

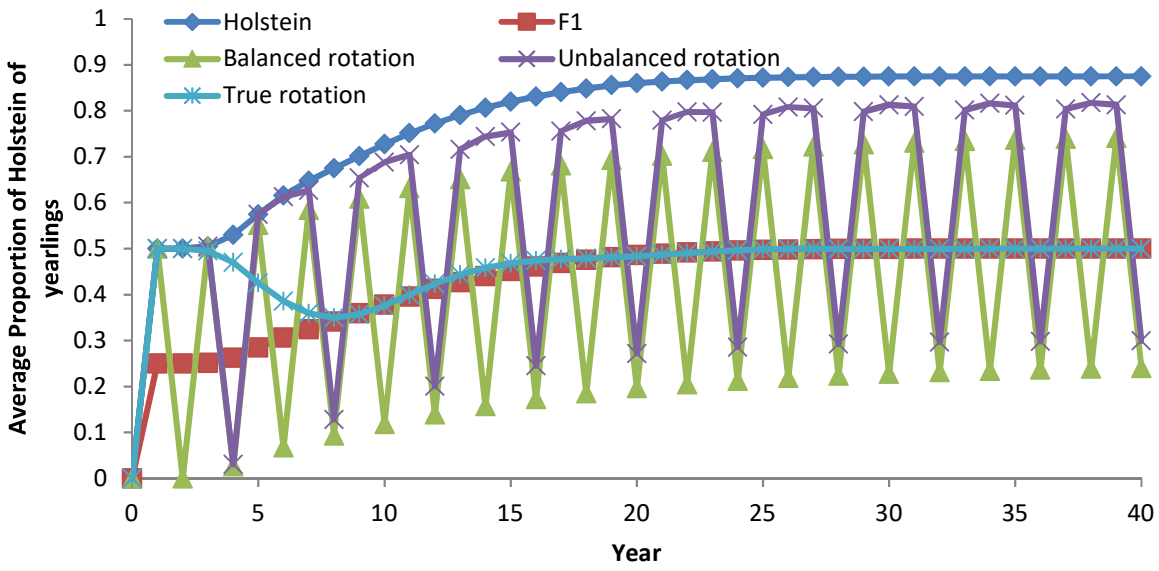
Figure 4.11. Average recombination of cows (>1 years of age) in herd, under the five crossbreeding strategies tested and over the 40 years modelled.



4.3.4 Genetic effects in yearlings

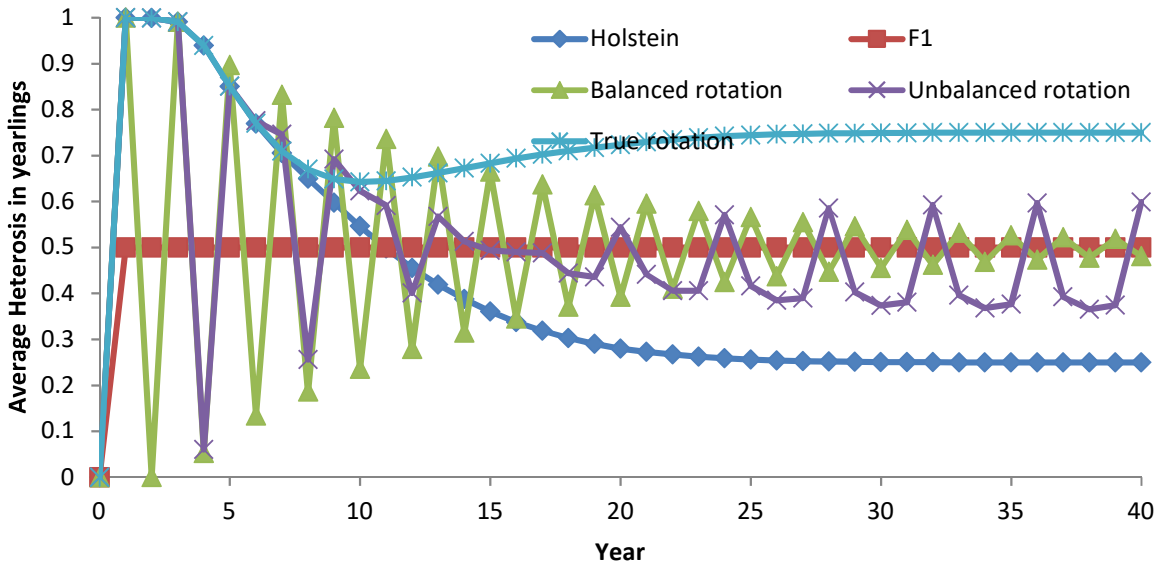
As with cows, the greatest proportion of Holstein genetics in yearlings was found under the Holstein sire strategy, the lowest under the F1 sire and balanced rotation strategies and the unbalanced rotation on average had an intermediate proportion of Holstein genetics in yearlings, between that of the Holstein and F1 sire strategies. However the yearly fluctuations under both the balanced and unbalanced rotation strategies are much greater for yearlings than for cows. As with cows, the proportion of Holstein genetics under the true rotation strategy initially followed that of the Holstein sire strategy, but by year 8, had reduced back to that of the F1 sire strategy (Figure 4.12).

Figure 4.12. Average proportion of Holstein genetics in yearlings under the five crossbreeding strategies tested and over the 40 years modelled.



Again, the average heterosis in yearlings for both the Holstein and F1 sire strategies was similar to the average heterosis in cows under these strategies. However the balanced and unbalanced rotation strategies showed much greater fluctuations in average heterosis for yearlings than for cows. The size of these fluctuations under both strategies decreased over time, with the balanced rotation, on average having similar levels of yearling heterosis to the F1 sire strategy and the unbalanced on average having slightly lower levels. Again, as for heterosis in cows, heterosis in yearlings under the true rotation strategy followed that of the Holstein sire strategy for years 0-8 and after this, did not show as large a decrease as under the Holstein sire strategy (Figure 4.13).

Figure 4.13. Average heterosis in yearlings under the five crossbreeding strategies tested and over the 40 years modelled.



4.3.5 Sensitivity analysis

Results of the sensitivity analysis for the genetic effects for milk yield showed that the ranking of strategies was robust. Neither increasing nor decreasing the size of the additive, heterosis or recombination effects by up to 10% led to any change in the ranking of strategies in terms of average milk yield. Results showed that a greater than 80% increase in the additive Holstein breed effect (the difference between E and L in the genetic model) was needed in order to change the ranking of strategies and this led to the Holstein sire strategy outperforming the true rotational strategy on average over years 0-40.

Results of the sensitivity analysis for the genetic effects for yearling weight similarly showed robust ranking of strategies. Neither increasing nor decreasing the size of the additive or heterosis effects by up to 10% led to any change in the ranking of strategies in terms of average yearling weight from years 0-40. When testing the inclusion of a negative

recombination loss for yearling weight, a value of at least 42% of the mean purebred was required to change the ranking of strategies. From this threshold, the F1 sire strategy led to lower average yearling weights than in the initial purebred Boran herd on average from years 0-40.

4.4 Discussion

In the present study we developed a model to predict how varying crossbreeding strategies affects the herd performance for a trait of interest. We illustrated the use of this model to examine the effects of five crossbreeding strategies over 40 years on an initial herd of Boran cattle in Ethiopia, studying two traits: milk yield and yearling weight. All five strategies tested led to an increase in both milk yield and yearling weight, partly due to the increase in the proportion of Holstein genetics in the herd and the positive additive Holstein breed effect for both traits. Going from a purebred to a crossbred herd also leads to the expression of heterosis which was positive for both traits. However, more advanced generations of crossbreds also tended to show greater recombination loss, which was greatest for milk yield.

Although some broad patterns were similar across the two traits, the results are also quite different, due to two factors. Firstly, the difference in the genetic effects for the two traits. The magnitude of the additive and heterosis effects for milk yield were much greater than for yearling weight, which explains the much greater increases in milk yield compared to yearling weight, under the same five strategies. The relative size and direction of additive and heterosis are the same for both traits, which may explain why the ranking of the strategies was broadly similar. The lack of a recombination effect for yearling weight meant

that for this trait, the F1 sire and balanced rotation strategies perform similarly on average; whereas for milk yield, the F1 sire strategy consistently performed slightly worse than the balanced rotation strategy due to the greater recombination loss. Secondly, the individuals in the herd that express these two traits are different. Yearling weight is always expressed by individuals of the same age that were sired by the bull used in the previous year, while milk yield is expressed by lactating cows of a range of ages (from 2-20 years) that were sired by bulls used over a longer time period, and so of different breed types, than the sires of yearlings. This explains why yearling weight tended to be much more sensitive to changes in sire type both in the first year and under the rotational strategies as the effect of a sire was seen more rapidly than in milk yield. For the balanced and unbalanced rotational strategies, where sires used were consistent within but changed across years, the difference between the traits is particularly clear, with the strategies leading to large fluctuations in yearling weight and much smaller fluctuations in milk yield.

4.4.1 Milk Yield

A common key aim of farmers crossbreeding local and exotic cattle is to increase milk yields (Cunningham and Syrstad, 1987; Chawala et al., 2019) as the amount of milk produced is directly linked to their income and profit. Typically, the exotic breed used to do this is the Holstein, due to its high milk yield and grading up to high proportion Holstein is common. However, our models showed that although the Holstein sire strategy was effective to increase and maximise milk yield for the first 10 years, predicted annual milk yields per cow dropped slightly from year 11 onwards. This reduction is due to a number of factors. Firstly, although the high proportion Holstein individuals that come into the herd after many years

of grading up do express high levels of the beneficial additive Holstein breed effect, they also express less beneficial heterosis and greater recombination loss than the earlier generations of crossbreds. Secondly, this trait is expressed as per cow in the herd and not all cows have a lactation in a year. The proportion of cows lactating in a year is determined by the proportion of cows calving in a year, as a lactation is begun by a cow calving. The proportion of cows calving in a year is determined by the age at first calving and calving interval. For both these fertility traits, there is a detrimental additive Holstein effect, meaning that crossbreds with more Holstein genetics have a lower chance of calving within a year and therefore a lower chance of beginning a lactation. In the later years under the Holstein sire strategy, a higher proportion of the herd are these high Holstein crossbreds with poorer fertility and therefore a greater proportion of the herd is not producing milk, thereby reducing the overall annual milk yield per cow.

Previous studies of local x exotic crossbreeds support our results that individuals with a high proportion of Holstein do not necessary produce more milk. In a study of cattle in Senegal, although there was a large increase in annual milk-offtake from indigenous zebu cattle compared to zebu-*Bos taurus* crossbreds (474L or 131% increase), the increase from moderate zebu-*Bos taurus* crossbreds to crossbreds with high levels of *Bos Taurus* was much smaller (107L) (Marshall et al., 2016). Similarly, in a study of Ankole-Holstein crossbred cattle in Burundi, milk yields of cows with more than 75% exotic genetics were only 1.6 times greater than those with 25% exotic genetics (Manirakiza et al., 2017) which is very similar to the value in our case study (1.8 times, see Figure 4.3). In a study of crossbred dairy cattle in Kenya it was found that under low production systems, individuals with a high proportion of exotic genetics (from European *Bos taurus* dairy breeds) did not have higher daily milk yields than crossbreds with a higher proportion of local genetics (Ojango et al., 2014). However, it

is worth noting that in the same study of crossbred cattle in Kenya, under high production systems, individuals with more than 60% exotic genetics were found to have significantly higher milk yields (Ojango et al., 2014), possibly due to a larger additive exotic breed effect or smaller heterosis effect under these conditions. This highlights the need to have genetic parameters that are specific not only to the pair of breeds of interest, but also the specific production system, when using our models. Results of our sensitivity analysis show ranking of strategies to be reasonably robust. However if the additive Holstein effect was significantly greater, the Holstein sire strategy would have continued to outperform the other strategies tested for the full timescale.

In systems where crossbred animals with a high proportion of the exotic breed do not necessary perform better than the intermediate crossbreds, strategies which lead to an average proportion of exotic genetics around 50% may be preferable. One way to achieve this is to grade up using a crossbred bull, as in the F1 sire strategy. Under this strategy, the proportion of Holstein genetics in the herd never rose above 50% and the rate of increase of milk yield was slower than most of the other strategies (Figures 4.4 and 4.9). Although the level of heterosis achieved by this strategy was more consistent than the Holstein sire strategy, it did not reach the same maximum level and this may have led to the poorest performance for milk yield of any of our strategies tested. However, another important factor is recombination. The F1 sire strategy led to the highest levels of recombination, double that of all other strategies in year 40. The expression of recombination in an individual is dependent on the level of crossbreeding in their parents. Although all strategies lead to crossbred dams after the first generation, the F1 sire strategy is the only one where sires used are also crossbred. As the recombination effect for milk yield was negative, this may explain why the F1 sire strategy showed the lowest increases. Similar to our results, in

reviews of crossbreeding in pigs and sheep, it has been found that the use of crossbred sires showed little or no effect on production traits (Buchanan, 1987; Leymaster, 1987). However in a simulation of goat crossbreeding in Kenya, it was found that the formation of a composite, where both sires and dams were crossbred, led to greater increases in meat production compared to rotational strategies where purebred sires were used (Mbuku et al., 2015).

The balanced rotational strategy led to a fluctuating but similar proportion of Holstein genetics and average heterosis in cows compared to the F1 sire strategy. However, the huge reduction in recombination under this strategy led to slightly higher milk yields compared to the F1 sire. The importance of considering recombination when designing breeding strategies for cattle in the tropics has been highlighted by Rutledge (2001), who in a meta-analysis of 80 taurine-indicine crossbreeding reports, found significant recombination load for annual milk yield. However, although this strategy did reduce the recombination expressed by cows compared to the F1 sire strategy, it still did not perform as well as the Holstein sire strategy.

The unbalanced rotation strategy, where sires used were Holstein for 3 years, followed by Boran for a single year, was designed as an intermediate between the Holstein sire and balanced rotational strategies, resulting in 75% Holstein genetics on average. It led to higher milk yields than the balanced rotational strategy because the herd moved from 0 to 50% Holstein, the change where the greatest milk yield benefit is seen, more quickly. Also, unlike the balanced rotational strategy, this strategy produces fewer individuals with less than 50% Holstein genetics. However, this strategy still results in less milk offtake compared to the Holstein sire strategy in the first 15 years, due to the smaller peak in heterosis under this strategy. Although, for years 21-40, the unbalanced rotational strategy does result in slightly

higher milk yields on average, due to the greater heterosis expressed by the herd during this period, compared to the Holstein sire strategy.

Both the balanced and unbalanced rotational strategies are not true rotational strategies because they alternated between sire types per year rather than per generation. Although there are practical benefits to this (in terms of reduced costs, but also operational convenience and simplicity), it does mean that they are not effectively maximising heterosis. The true rotation strategy led to the maximum heterosis of any strategy tested over every year tested, which led to the greatest average annual milk yield over the first and second halves of the time period. Only from years 10-16 did the Holstein sire strategy lead to slightly higher annual milk yields per cow. During these years, average heterosis of cows dipped slightly, before rising again, which explains this small dip in predicted milk yields.

4.4.2 Yearling Weight

Unlike milk yield, the desired direction of change for yearling weight is less clear. Although heavier surplus yearlings may led to greater income through selling as live animals or meat production, yearling weight may also be considered as a proxy for rearing costs. Therefore by minimising yearling weight increases, farmers can minimise rearing costs, increasing profits. In selection indices for Australian Holstein cattle there is a negative weight for body weight, suggesting a negative desired direction of change, as lighter animals require a smaller maintenance feed cost (Pryce et al., 2015; Byrne et al., 2016). However in a selection index designed for Boran cattle in Kenya, a positive weight is used for yearling weight (Rewe et al., 2010) because the index is designed to increase meat yields. If we consider milk rather than meat as the primary output from our case study system, this may be less relevant. In a

survey of Tanzanian smallholder dairy farmers, it was found that farmers preferred smaller cattle (Chawala et al., 2019), due to their reduced maintenance feed costs and as this system is more similar to the one modelled in this study, we assumed that a lower yearling weight would be preferable.

As with milk yield, the Holstein additive and heterosis effects for yearling weight were positive and all strategies increase the proportion of Holstein genetics and expression of heterosis compared to the initial purebred Boran herd. This meant that all strategies led to an increase in yearling weight compared to the initial herd. These increases are consistent with a survey of farms in Ethiopia which found that crossbred cattle tended to need higher levels of nutrition than animals of local breeds (Bitew et al., 2012). The Holstein sire strategy led to the highest yearling weights. Crossbreds with the greatest yearling weights are the F1s, due to the heterosis effect being more than half the size of the additive Holstein effect for this trait. The Holstein sire achieves this maximum in year 1 as all yearlings are F1s. In subsequent years, the performance of other crossbreds with more than 50% Holstein genetics was very similar to the F1s, meaning that the average yearling weight for years 1-40 remains at approximately this same high level. Compared to the Holstein sire strategy, the F1 sire strategy led to smaller increases in average yearling weight due to lower levels of both the additive Holstein and heterosis effects. The balanced and unbalanced rotational strategies led to larger fluctuations in yearling weight from similar levels to the Holstein sire strategy to below that of the F1 sire strategy, with the unbalanced sire having greater weights on average due to greater expression of the Holstein additive effect. These fluctuations were due to changing sire type frequently and so changing breed proportions quickly. These fluctuations are not desirable for farmers as they would need to change the

management required often and years of increased feed demand wouldn't necessarily follow years when more feed was available.

Results for the true rotation strategy were initially similar to the Holstein sire strategy but decreased again as the proportion of Holstein in yearlings decreased again. It did not have the annual fluctuations of the other rotational strategies because in this strategy, not all yearlings are sired by the same sire type in a year, making this strategy preferable for farmers who want a more consistent feed cost.

4.4.3 Optimal strategy

The best strategy for increasing milk yield was the true rotation strategy because it takes advantage of large beneficial Holstein additive and heterosis effects. Conversely, the best strategy for minimizing increases in yearling weight was the F1 sire strategy as it led to the smallest increases in Holstein additive and heterosis effects. This means a farmer must trade-off between these two traits. How this is done is dependent on relative importance of these traits and other traits not examined here. This relative importance can be assessed using a number of methods, for example by using farmer opinion (Nielsen and Amer, 2007; Chawala et al., 2019), by building an economic model (Byrne et al., 2016) or by building models that takes into account other factors, for example greenhouse gas emissions (Wall et al., 2010) and varying weights for each trait can be used to develop an index. This can then be used to identify an optimal strategy.

When deciding an optimal strategy, the practicalities and costs of implementing the strategy must also be considered. Strategies where a single sire type is used for all females are simpler to implement, partly because all cows can be mated to the same bull, but also

because these strategies do not require any pedigree recording for cows. This is not the case for the true rotation strategy and therefore may reduce its appeal for farmers.

Our results highlight the importance of considering both the additive and non-additive genetic effects when designing crossbreeding strategies. This was particularly the case when considering milk yield for our case study of Boran-Holstein crossbreeding in Ethiopia. Despite the huge Holstein additive genetic effect for this trait, a strategy that maximised heterosis rather than proportion Holstein performed best.

Chapter 5: Crossbreeding cattle in sub-Saharan Africa: Modelling profitability and greenhouse gas emissions under varying strategies

5.1 Introduction

Livestock are an important source of both income and food security for people across sub-Saharan Africa (SSA). The potential for income and the importance of livestock for food security will increase as demand for animal products increases with the large predicted increases in population size in the region (Haub and Kaneda, 2013). Cattle are an important species, as dairy has been shown to be an area with particularly great potential for growth to meet this increase in demand (Wood et al., 2006), in part due to the large gaps between potential and realised production levels (Henderson et al., 2016).

However, globally, livestock farming has a significant contribution to GHG emissions, accounting for around 15-18% of the total GHG produced (FAO, 2013; Opio et al., 2013). The majority of these emissions (64-78%) are due to cattle farming (Gerber et al., 2013; Herrero et al., 2013b). In developing countries these emissions are increasing. Between 1961 and 2010 the livestock emissions in developing countries, including those in SSA, increased by 117% (compared to a decrease of 23% in developed countries), largely due to an increase in methane emissions from beef and dairy cattle production (Caro et al., 2014). Emission intensity for milk production in SSA is thought to be one of the worst of any region of the world, estimated to be around 9 kg CO_2eq/kg, compared to 1.6 kg CO_2eq/kg in Western Europe (Opio et al., 2013) due to low production levels as well as other inefficiencies.

Therefore there is a need to increase food production and profitability of cattle farms whilst not increasing GHG emissions. Crossbreeding is considered a good strategy for SSA to increase production and profitability, as it allows farmers to take advantage of

complementary robustness traits from local breeds and production traits from exotics (Cunningham and Syrstad, 1987), as well as providing favourable heterosis (as shown in chapter 2).

In previous chapters, models were described and tested which predict herd performance for individual traits under varying crossing strategies. However, to identify an optimal strategy for a system, we need to assess how a strategy performs for multiple traits simultaneously and also how these traits combine to assess the effect of crossbreeding strategies on herd profitability and greenhouse gas emissions. The objective of this chapter is to describe economic and GHG models, based on the tier II IPCC framework (IPCC, 2006) and use the models to predict the results of a variety of crossbreeding strategies in a case study system of Boran-Holstein crossbreeding in Ethiopia, thereby addressing the fourth and fifth objectives of the thesis.

5.2 Materials and Methods

The herd model from the previous chapter is used to calculate the effect of variation in crossbreeding strategy on the annual herd composition, in terms of what types of crossbred animals, at what ages, are present within the herd each year. Herd composition is then used to predict annual profit and GHG emissions for the herd, under varying crossbreeding strategies, using economic and GHG models respectively.

5.2.1 Case study: Boran x Holstein in Ethiopia

To test the model, a case study of smallholder cattle farming in Ethiopia is used. A common local breed in this region is the Boran, a dual-purpose (both milk and meat) zebu breed. Crossbreeding scenarios which use Boran, Holstein and F1 (from a Boran dam and Holstein

sire) bulls are tested. Holstein sires are used via artificial insemination and semen is imported to Africa with the aim of increasing milk yields of local cattle. Long-term crossbreeding studies between Boran and Holstein cattle in Ethiopia (Haile et al., 2008, 2009a; b, 2011) provide many of the genetic input parameters needed to predict the performance of crossbred individuals. Also, a focus in the country on improving cattle farming (Shapiro et al., 2015) has led to many surveys recording parameter values needed for economic and greenhouse gas emissions modelling.

The five crossbreeding strategies tested are the same as those tested in the previous chapter (Table 4.1). Firstly, two strategies that use a single type of sire for all females over all years, either a Holstein or F1 sire, are tested. Secondly, two strategies that rotated sire types among years: a balanced rotation where the sire used swaps between Holstein and Boran every year and an unbalanced rotational strategy where a Holstein sire was used for 3 years, followed by a Boran for a single year, with this pattern repeated, are tested. Finally, a true rotation strategy where the sire used on a given female depended on the ancestry of that female, is considered. Cows sired by a Boran were mated to a Holstein, whereas cows sired by a Holstein were mated to a Boran sire, meaning that the sire used rotated every generation rather than every year.

5.2.2 Economic model

The annual profit for a given year (Y), $Profit_Y$, was calculated by subtracting $Costs_{i,Y}$, the total annual costs associated with animal type in year Y, from $Income_{i,Y}$, total annual income in year Y associated with animal type i and summing across animal types.

$$\text{Profit}_Y = \sum_i \text{Income}_{i,Y} - \text{Costs}_{i,Y}$$

Animal type (i) includes all those listed in table 5.1 and the calculations of income and costs from each are described below.

Table 5.1. All animal types and their definitions. Note that a single animal can move between types from one year to the next. A single animal may also appear in multiple types, for example, DRY and LAC are subsets of COW and REP, SREP and FIN are subsets of Y1.

Animal type	Definition
COW	all animals (only females) 2 years and older, alive in the herd
DRY	all cows that do not give birth
LAC	all cows that calve and so begin a lactation
CULL	all cows that leave the herd in a year
LCALF	all animals that live to 1 year old
DCALF	all animals that die between birth and 1 year old
REP	all animals between 1 and 2 years old that are being kept as replacement females
SREP	all females that live to 1 year old but are not kept as replacement females so are sold
FIN	all males that live to 1 year old and are sold

5.2.2.1 Cows

The costs associated with all adult cows in the herd (irrespective of whether they are lactating or not) are dependent on the herd composition and the varying labour and health costs associated with different crossbred types.

$$\text{Costs}_{COW,Y} = \sum_{C=1}^{18} N_{COW,C,Y}(Labour_C + Health_C)$$

$N_{COW,C,Y}$ is dependent on the herd composition in a year and is equal to the number of animals of type COW and crossbred type C, present in the herd in year Y. For definitions of crossbred types, see the previous chapter.

$Labour_c$ is the annual labour cost and $Health_c$ is the annual costs for health associated with a crossbred of type C. Breed and breed cross differences in labour and many other cost and revenue factors are calculated using a genetic crossbreeding model (Dickerson, 1973) which considers the additive, heterosis and recombination loss effects (L, E, H and R) for the trait for crosses of the specific pair of breeds and in a specific system (see table 3 for parameter values for all traits modelled this way). These values are produced by long term crossbreeding studies. These are then weighted (al, ae, h and r) depending on the crossbred type (see Table 2 for parameter values for all crossbred types), to predict the performance of that crossbred for the trait of interest. Thus

$$\mathrm{Labour_C} = \mathrm{al_C}\, L_{\mathrm{Labour}} + \mathrm{ae_C} E_{Labour} + h_C H_{Labour} + r_C R_{Labour}$$

and

$$\mathrm{Health_C} = al_C\, \mathrm{L_{Health}} + \mathrm{ae_C}\, \mathrm{E_{Health}} + h_C H_{Health} + r_C R_{Heal} \quad .$$

There is no income associated with this animal type as all income is accounted for elsewhere.

$$\mathrm{Income}_{COWS,Y} = 0$$

5.2.2.2 Dry cows

The costs associated with dry cows are dependent on the number of animals of this type and of each crossbred type in the herd, the feed costs associated with dry cows and the price of feed. Costs for dry cows in a given year are calculated as:

$$\mathrm{Costs}_{DRY,Y} = \sum_{C=1}^{18} N_{DRY,C,Y} \times Feed_{DRY,C} \times Feedprice$$

$N_{DRY,C,Y}$ is dependent on the herd composition in a year and is equal to the number of animals of type DRY and crossbred type C, present in the herd in year Y.

Feedprice is the cost of 1 kg of dry matter of cattle feed. For Ethiopia, a value of 0.7 Ethiopian Birr /kg (Dejene et al., 2014) was used.

$Feed_{DRY,C}$ is the amount of feed required in kg of dry matter, by dry cows of crossbred type C. It includes the feed requirements associated with maintenance only and is calculated as:

$$Feed_{DRY,C} = \frac{\left(\frac{NE_{M,DRY,C}}{REM}\right)}{DEofFeed}$$

REM, the ratio of net energy available in diet for maintenance to digestible energy consumed, is calculated using equation 10.14 from IPCC guidelines.

DEofFeed is the digestible energy in MJ per kg of dry matter of feed as is dependent on the system being studied. For Ethiopia, a value of 7.1 MJ of metabolisable energy (Bogale et al., 2008), was converted to digestible energy, by dividing by 0.81 (CSIRO, 2007), giving a value of 8.77 $MJkg^{-1}$.

Net energy required for maintenance for dry cows is calculated using the equation below (as in IPCC equation 10.3 and table 10.4).

$$NE_{M,DRY,C} = (MW_C)^{0.75} \times 0.322$$

MW_C, the mature weight of a crossbred type C, is estimated similarly to previous traits using a genetic model, giving the equation below. For parameter values, see Tables 5.2 and 5.3.

$$MW_C = ax_C L_{MW} + ay_C E_{MW} + h_C H_{MW} + r_C R_{MW}$$

There is no income associated with this animal type as it is accounted for elsewhere.

$$\text{Income}_{DRY,Y} = 0$$

5.2.2.3 CALVING COWS

Costs associated with cows that calve and so begin a lactation, in a given year, are dependent on the herd composition, feed requirements associated with this animal type and the cost of feed and is calculated as:

$$\text{Costs}_{LAC,Y} = \sum_{C=1}^{18} N_{LAC,C,Y} \times Feed_{LAC,C} \times Feedprice$$

$N_{LAC,C,Y}$ is dependent on the herd composition in a year and is equal to the number of animals of type LAC and crossbred type C, present in the herd in year Y.

$Feed_{LAC,C}$ is the amount of feed required in kg of dry matter, by the animal type LAC (cows that calve and so begin a lactation) of crossbred type C. It includes the feed requirements associated with maintenance, lactation and pregnancy and is calculated as:

$$Feed_{LAC,C} = \frac{\left(\frac{NE_{M,LAC,C} + NE_{l,LAC,C} + NE_{p,LAC,C}}{REM}\right)}{DEofFeed}$$

Net energy required for maintenance for lactating cows ($NE_{M,LAC}$) is calculated using the equation below (as in IPCC equation 10.3 and table 10.4).

$$NE_{M,LAC,C} = (MW_C)^{0.75} \times 0.386$$

Net energy required for lactation ($NE_{l,LAC}$) is calculated using the equation below (as in IPCC equation 10.8).

$$NE_{l,LAC,C} = Milk_C\,(1.47 + 0.4Fat_C)$$

$Milk_C$ and Fat_C, the lactation milk yield in kg and fat percentage of milk for crossbred type C respectively, are calculated again using a genetic model.

$$Milk_C = al_C L_{Milk} + \text{a}eE_{Milk} + h_C H_{Milk} + r_C R_{Milk}$$

$$Fat_C = al_C L_{Fat} + ae_C E_{Fat} + h_C H_{Fat} + r_C R_{Fat}$$

Net energy required for pregnancy ($NE_{p,LAC}$) is calculated using the equation below (as in IPCC equation 10.13 and table 10.7).

$$NE_{p,LAC,C} = 0.1 \times (MW_C)^{0.75} \times 0.386$$

Finally, income associated with lactating females in year Y, is dependent on the number of females beginning a lactation in a year, the amount of milk produced in a lactation and the price received per kg of milk and calculated as follows:

$$\text{Income}_{LAC,Y} = \sum_{C=1}^{18} N_{LAC,C,Y} \times Milk_C \times Milkprice$$

Milkprice is the price per kg of milk. For Ethiopia, a value of 5.1 Ethiopian Birr per kg (Chagwiza et al., 2016) was used.

5.2.2.4 CULL COWS

There are no costs associated with animals that leave the herd within a year

$$\text{Costs}_{CULL,Y} = 0$$

Income associated with cows that leave the herd in a given year, is dependent on the herd composition, the value of animals if sold and the proportion of animals that leave that are sold and is calculated as:

$$\text{Income}_{CULL,Y} = \sum_{C=1}^{18} N_{CULL,C,Y} \times Cowvalue_C \times PCullSold$$

$N_{CULL,C,Y}$ is dependent on the herd composition in a year and is equal to is the number of animals of type CULL and crossbred type C, present in the herd in year Y.

PCullSold is the proportion of animals that leave the herd that are sold. For Ethiopia, a value of 0.4 (Asfaw and Jabbar, 2008) was used. Animals not sold are assumed to have died on farm.

$Cowvalue_C$ is the value of a cow of crossbred type C and is calculated using a genetic model (see Tables 5.2 and 5.3 for input parameters).

$$Cowvalue_C = al_C L_{Cowvalue} + ae_C E_{Cowvalue} + h_C H_{Cowvalue} + r_C R_{Cowvalue}$$

5.2.2.5 LIVE CALVES

Cost associated with calves that live until a year of age, are dependent on the herd composition, feed requirements associated with this animal type and the cost of feed and is calculated as:

$$\text{Costs}_{LCALF,Y} = \sum_{C=1}^{18} N_{LCALF,C,Y} \times Feed_{LCALF,C} \times Feedprice$$

$\text{Feed}_{LCALF,C}$ is the amount of feed required in kg of dry matter, by calves that live to one year old and of crossbred type C. It includes the feed requirements associated with maintenance and growth and is calculated as:

$$Feed_{LCALF,C} = \frac{\left(\frac{NE_{M,LCALF,C}}{REM}\right) + \left(\frac{NE_{G,LCALF,C}}{REG}\right)}{DEofFeed}$$

REG is calculated using equation 10.15 from IPCC guidelines.

The net energy required for maintenance of calves is estimated using the following:

$$NE_{M,LCALF,C} = \sum_{d=0}^{365} (CW_C)^{0.75} \times 0.322$$

Where $\text{CW}_{C,d}$ is the liveweight of calves of crossbred type C on day d and for d between 0 and 364, is calculated using the following:

$$CW_{C,d} = BW_C + (d \times CWG_c)$$

BW_C is the birth weight of crossbred type C and is calculated using a genetic model:

$$BW_C = al_C L_{BW} + ae_C E_{BW} + h_C H_{BW} + r_C R_{BW}$$

CWG is the average daily weight gain of calves from birth to 1 year old and is calculated as:

$$CWG_C = \frac{(YW_C - BW_C)}{365}$$

YW_C is the yearling weight of crossbred type C and is calculated using a genetic model:

$$YW_C = al_C L_{YW} + ae_C E_{YW} + h_C H_{YW} + r_C R_{YW}$$

BW_C is the birth weight of crossbred type C and is calculated using a genetic model:

$$BW_C = al_C L_{BW} + ae_C E_{BW} + h_C H_{BW} + r_C R_{BW}$$

The net energy required for growth of calves is estimated using the following:

$$NE_{G,LCALF,C} = \sum_{d=0}^{365} 22.02 \left(\frac{CW_{C,d}}{MW_C}\right)^{0.75} {WG_C}^{1.097}$$

There is no income associated with this animal type as any is accounted for elsewhere.

$$\text{Income}_{LCALF,Y} = 0$$

5.2.2.6 Dead calves

The costs associated with calves that die between 0 and 1 years of age are calculated as those for live calves, except that the total cost is reduced to account for animals not being alive, and therefore not needing feed for the full year.

$$\text{Costs}_{DCALF,Y} = \sum_{C=1}^{18} N_{DCALF,C,Y} \times Feed_{LCALF,C} \times Feedprice \times deathage_C$$

Where $deathage_C$ is the average age of death of calves that die between birth and 1 year, measured in years. For Ethiopia, a value of 0.5 years was used.

There is no income associated with this animal type.

$$\text{Income}_{DCALF,Y} = 0$$

5.2.2.7 Replacement females

Cost associated with heifers that are kept as replacements are dependent on the herd composition, feed requirements associated with this animal type and the cost of feed and is calculated as:

$$\text{Costs}_{REP,Y} = \sum_{C=1}^{18} N_{REP,C,Y} \times Feed_{REP,C} \times Feedprice$$

$Feed_{REP,C}$ is the amount of feed required in kg of dry matter, by heifers from ages 1-2 years of crossbred type C. It includes the feed requirements associated with maintenance and growth and is calculated as:

$$Feed_{REP,C} = \frac{\left(\frac{NE_{M,REP,C}}{REM}\right) + \left(\frac{NE_{G,REP,C}}{REG}\right)}{DEofFeed}$$

The net energy required for maintenance of replacement heifers is estimated using the following:

$$NE_{M,REP,C} = \sum_{d=365}^{730} (HW_C)^{0.75} \times 0.322$$

Where $HW_{C,d}$ is the liveweight of heifers of crossbred type C on day d and for d between 365 and 730, is calculated using the following

$$HW_{C,d} = BW_C + ((d - 365) \times HWG_c)$$

Where $HWG_{C,d}$ is the weight gain of heifer of crossbred type C from day = d-1 to day = d between day 365 and 730 of life and is calculated using the following:

$$HWG_C = \frac{(MW_C - YW_C)}{365}$$

The net energy required for growth of calves is estimated using the following:

$$NE_{G,REP,C} = \sum_{d=365}^{730} 22.02 \left(\frac{HW_{C,d}}{MW_C}\right)^{0.75} {HWG_{C,d}}^{1.097}$$

There is no income associated with this animal type.

$$\text{Income}_{DCALF,Y} = 0$$

5.2.2.8 SURPLUS REPLACEMENT FEMALES

As they are accounted for elsewhere, there are no specific costs associated with surplus heifers that are sold at 1 year of age.

$$\text{Costs}_{SREP,Y} = 0$$

Income associated with surplus heifers, is dependent on the herd composition and the sale value of heifers and is calculated as:

$$\text{Income}_{SREP,Y} = \sum_{C=1}^{18} N_{SREP,C,Y} \times Heifervalue_C$$

Heifervalue_C is the value of a heifer of crossbred type C and is calculated using a genetic model (see Tables 5.2 and 5.3 for input parameters).

$$Heifervalue_C = al_C L_{Heifervalue} + ae_C E_{Heifervalue} + h_C H_{Heifervalue} + r_C R_{Heifervalue}$$

5.2.2.9 SURPLUS MALES

As they are accounted for elsewhere, there are no specific costs associated with surplus males that are sold at 1 year of age.

$$\text{Costs}_{FIN,Y} = 0$$

Income associated with surplus males, is dependent on the herd composition and the sale value of yearling males and is calculated as:

$$\text{Income}_{FIN,Y} = \sum_{C=1}^{18} N_{FIN,C,Y} \times Oxvalue_C$$

Oxvalue_C is the value of a yearling male of crossbred type C and is calculated using a genetic model (see Tables 5.2 and 5.3 for input parameters).

$$Oxvalue_C = al_C L_{Oxvalue} + ae_C E_{Oxvalue} + h_C H_{Oxvalue} + r_C R_{Oxvalue}$$

Table 5.2. Weights for genetic effects for each crossbred type. a_l and a_e are equal to the proportions of local and exotic breed respectively, in the crossbred type. h is the proportion of maximum heterosis expressed by the crossbred type. r is a measure of the average amount of recombination that has occurred between parental haplotypes and is equal to the mean fraction of independently segregating pairs of loci in gametes from both parents that are expected to be different from that found in either purebred.

Crossbred type	al	ae	h	r
1	1	0	0	0
2	0.5	0.5	1	0
3	0.75	0.25	0.5	0.25
4	0.75	0.25	0.5	0.25
5	0.25	0.75	0.5	0.25
6	0.5	0.5	0.5	0.5
7	0.875	0.125	0.25	0.1875
8	0.375	0.625	0.75	0.1875
9	0.625	0.375	0.5	0.4375
10	0.875	0.125	0.25	0.1875
11	0.375	0.625	0.75	0.1875
12	0.625	0.375	0.5	0.4375
13	0.625	0.375	0.75	0.1875
14	0.125	0.875	0.25	0.1875
15	0.375	0.625	0.5	0.4375
16	0.75	0.25	0.5	0.25
17	0.25	0.75	0.5	0.25
18	0.5	0.5	0.5	0.5

Table 5.3. Genetic parameters for traits included in the model for crossbreeding between Boran (local breed) and Holstein (exotic breed) cattle in Ethiopia. L and E are the average performance of the local and exotic breeds, respectively. H is the maximum heterosis and R the maximum recombination loss.

Trait	Unit	L	E	H	R
Lactation milk yield	kg	447.73	2487.92	899.02	-586.44
Fat %	%	5.01	3.56	0.54	
Protein %	%	3.6	2.63	0.25	
Birth weight	kg	23.3	31.4	-1.5	
Yearling weight	kg	111.2	146.8	17.9	
Mature weight	kg	304	444	8	-68
Heifer value	BIR	3811	18000		
Ox value	BIR	14111	17000		
Labour cost per cow	BIR	418	836		
Health & AI costs	BIR	2.366	22.222	-9.052	
Cow value	BIR	4955	28000		

5.2.3 GHG Model

The 2006 IPCC Guidelines were used to estimate annual methane and nitrous oxide emissions according to the varying herd compositions predicted in the previous chapter under varying crossbreeding strategies. Total methane emissions for each year was calculated by summing the total enteric methane emissions and the total methane emissions from manure each year.

Total enteric methane emissions are dependent on the herd composition and the emission factors for each crossbred type within each animal type. They were calculated using the following:

$$\text{Total enteric methane emissions}_Y = \sum_i \sum_{C=1}^{18} \left(N_{C,i,Y}\, EF_{C,i}\right)$$

$EF_{C,i}$ is the emission factor, or the predicted annual enteric methane emissions for a crossbred type C and animal type i. These were calculated following IPCC tier II guidelines, by first calculating annual gross energy feed requirements for all crossbred and animal types using IPCC equation 10.16 and a value of 65% for digestible energy expressed as a percentage of gross energy (DE%). This value was used as it falls within the suggested values in Table 10.2 in the IPCC guidelines and was also used by authors modelling similar systems in SSA (Weiler et al., 2014). Then IPCC equation 10.21 was used along with a methane conversion factor (Y_m) to estimate emission factors.

Total methane emissions from manure are dependent on the herd composition and the emission factors for each crossbred type within each animal type. They were calculated using the following:

$$\text{Total methane emissions from manure}_Y = \sum_i \sum_{C=1}^{18} \left(N_{C,i,Y}\, Methane\ emissions\ from\ manure_{C,i}\right)$$

Annual methane emissions from manure were estimated for each animal type and crossbred type using IPCC equations 10.23 and 10.24 and input parameters from IPCC tables 10A-4 and 10A-9.

Annual direct and indirect N_2O emissions from manure were then estimated for each animal type and crossbred type using IPCC equations 10.25 and 10.26, respectively.

$$\text{Total N2O emissions from manure}_Y$$

$$= \sum_i \sum_{C=1}^{18} \left(N_{C,i,Y} \left(Direct\ N_2O\ emissions\ from\ manure_{C,i}\right.\right.$$

$$\left.\left. + \ Indirect\ N_2O\ emissions\ from\ manure_{C,i}\right)\right)$$

Annual nitrogen excretion rates were estimated for each animal type and crossbred type using IPCC equations 10.31, 10.32 and 10.33. These required milk protein percentages for each crossbred type and this was estimated using a genetic model:

$$Protein_C = \ ax_C L_{Protein} + ay_C E_{Protein} + h_C H_{Protein} + r_C R_{Protein}$$

Finally, before summing, total annual methane and nitrous oxide were weighted according to their 100 year global warming potential (Myhre et al., 2013), depending on their ability to trap heat in the atmosphere compared to the standard of carbon dioxide, allowing results to be expressed in kg of CO_2 equivalents (265 and 28, respectively).

5.2.4 Emission Intensity

In order to measure the effect of crossing strategy on GHG emissions and production level simultaneously, the annual emission intensity (EI) of milk production under each strategy was also considered. The benefit of EI is it can be used to identify strategies that allow for a decrease in emissions whilst maintaining a constant production level, or an increase in productivity whilst maintaining current emission levels. The EI of milk production was calculated for each strategy. The annual GHG emissions, measured in kg of CO_2 equivalents per cow was divided by the annual fat and protein corrected milk (FPCM) yield per cow, to give at EI measured in kg of CO_2 per kg FPCM.

5.2.5 Cost of Carbon

A weakness of using EI is that it is expressed on a scale that is not relevant for farmers. An alternative is to apply a shadow price to GHG emissions in the form of a carbon tax. Due to the intense global interest in GHG emissions, this strategy has been considered to reduce GHG emissions from ruminant farming in a range of countries (e.g. China (Shi et al., 2019) and France (Mosnier et al., 2017)). Carbon taxes have also been considered for countries in sub-Saharan Africa. One study considered a carbon tax for Ethiopia of 30 US dollars per tonne of CO_2, although authors did not apply this to food production (Telaye et al., 2019). 30 US dollars is approximately equal to 870 Ethiopian Birr and this additional cost per tonne of CO_2 equivalents was included in the profitability model, to estimate the annual profit after carbon tax per cow for each strategy.

5.3 Results

Table 5.4. Annual profit per cow, global warming potential (GWP) per cow, emission intensity (EI) of fat and protein corrected milk (FPCM) and annual profit - carbon tax per cow for the initial herd of purebred Boran and under the five strategies tested, averaged over years 0-40. Numbers in brackets show the rankings of each strategy for that metric with 1 being the best and 5 the worst.

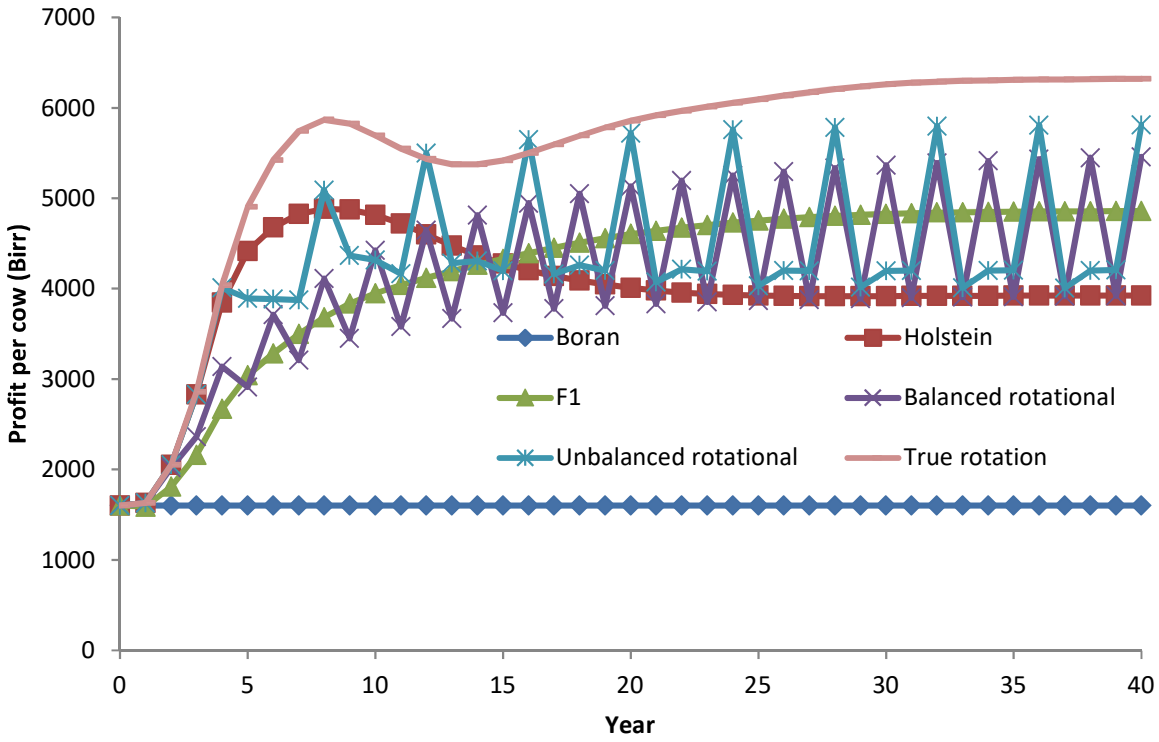
Strategy	Annual profit per cow (Birr)	GWP per cow (kg CO_2 equivalents)	EI of milk (kg CO_2 per kg FPCM)	Annual profit - C tax per cow (Birr)
Boran herd	1604	1260	5.57	508
Holstein sire	3953 (5)	1710 (5)	2.37 (3)	2465 (5)
F1 sire	4164 (3)	1509 (1)	2.47 (5)	2852 (2)
Balanced rotational	4105 (4)	1574 (2)	2.41 (4)	2736 (4)
Unbalanced rotational	4274 (2)	1664 (3)	2.30 (2)	2827 (3)
True rotation	5499 (1)	1673 (4)	2.03 (1)	4044 (1)

5.3.1 Profitability

All strategies increased annual profits compared to that of purebred Boran herd (1604 Birr per cow) (See Figure 5.1 and Table 5.4). The Holstein sire strategy led to one of the fastest increases in profit for the first four years, after which the rate of increase slowed, reaching a maximum of 4885 Birr per cow in year 8 and then reducing and stabilising to around 3920 Birr per cow after 25 years. Over the whole period tested (years 0-40), this led to an average

annual profit of 3953 Birr per cow. The F1 sire strategy increased annual profits at a slower initial rate but from year 15 onwards, annual profits under this strategy were predicted to be greater than under the Holstein sire. The rate of increase slowed over time reaching a maximum of 4861 Birr per cow in year 40. Over the whole period tested, this led to an average annual profit of 4164 Birr per cow. The balanced rotational strategy performed, on average, very similarly to the F1 sire strategy, with an average annual profit of 4105 Birr per cow over years 0-40. However, under this strategy annual profits were predicted to fluctuate yearly. The size of these oscillations increased over the 40 years, with annual profits per cow predicted to be 3924 and 5461 Birr in years 39 and 40 respectively. The unbalanced rotational strategy also led to oscillations in predicted annual profits. However, on average it led to higher annual profits than the balanced rotational strategy (4274 Birr per cow), with greater peaks and lower troughs. Peaks only occurred every 4 years, rather than every 2 as predicted under the balanced strategy. The true rotation strategy led to the highest annual profits on average from years 0-40 (5499 Birr per cow). It led to a fast initial increase from years 0-8, reaching an annual profit of 5869 Birr per cow in year 8. From years 8 – 14, annual profits were predicted to drop slightly, but after this they rose again, reaching a maximum of 6325 Birr per cow in year 40, a 3.9 fold increase from the initial herd in year 0.

Figure 5.1. Annual profit per cow in the herd from years 0-40 under the 5 strategies tested and compared to a baseline of a herd of purebred Boran.

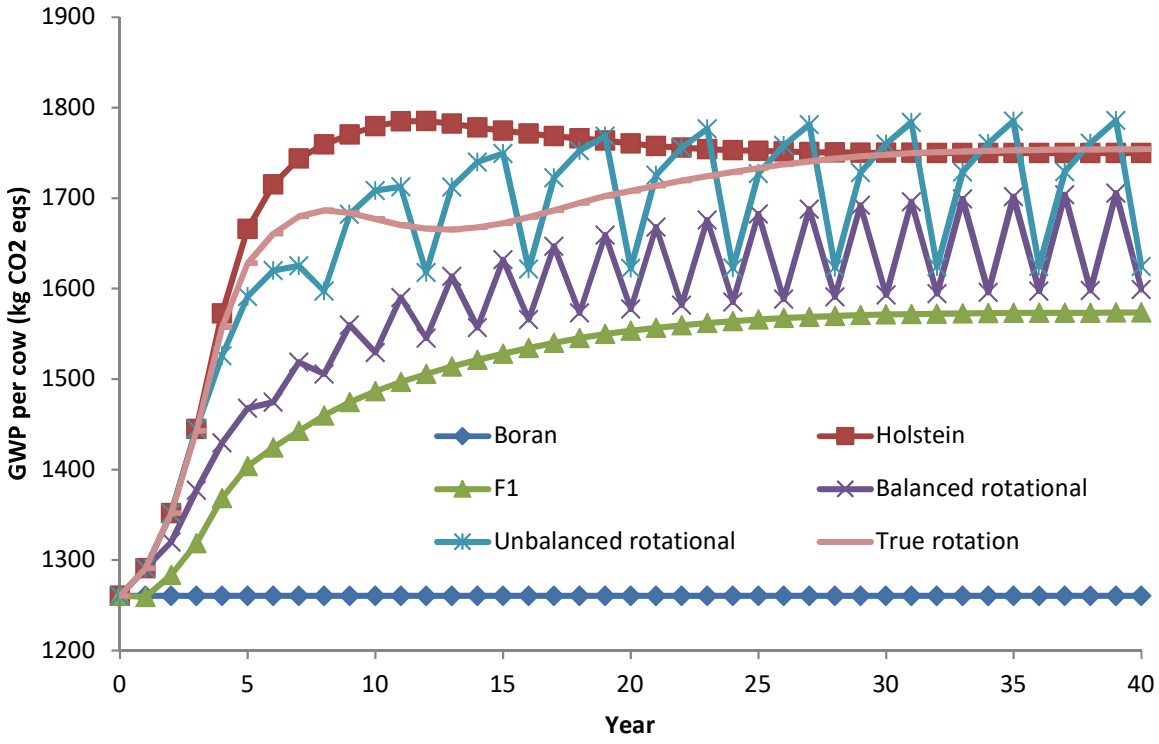


5.3.2 GHG Emissions

Again, all strategies tested increased GHG emissions compared to the initial herd of purebred Borans, which was estimated as 1260 kg CO_2 equivalents per adult cow per year (see Figure 5.2 and Table 5.4). The Holstein sire strategy had the largest average annual GHGs emissions over years 0-40 (1710 kg CO_2 equivalents per cow). It led to the greatest rate of increase which reduced over time, reaching a peak of 1778 kg CO_2 equivalents in year 14 and then reducing slightly and stabilising at 1750 kg in year 29. This contrasts with the results for the F1 sire strategy, which led to the smallest increases in GHG emissions of all the strategies tested, only reaching 1574 kg CO_2 equivalents per cow in year 40. The balanced rotational strategy led to fluctuating levels of GHG emissions but remained

between those predicted under the Holstein and F1 sire strategies, resulting in average annual emissions of 1574 kg CO_2 equivalents per cow. The unbalanced rotational strategy led to similar although less frequent and more extreme fluctuations, but consistently higher emissions. From year 23 onwards, this strategy led to peaks in annual emissions that were greater than those predicted under the Holstein sire strategy, although on average across years 0-40, this strategy did lead to lower annual emissions (1663 kg CO_2 equivalents per cow). Emissions for the true rotational strategy began and finished similar to those predicted under the Holstein sire strategy. However the lower emissions predicted for years 4-28 under this strategy meant that on average over years 0-40, the true rotation strategy led to lower annual emissions (1673 kg CO_2 equivalents per cow) compared to the Holstein sire strategy.

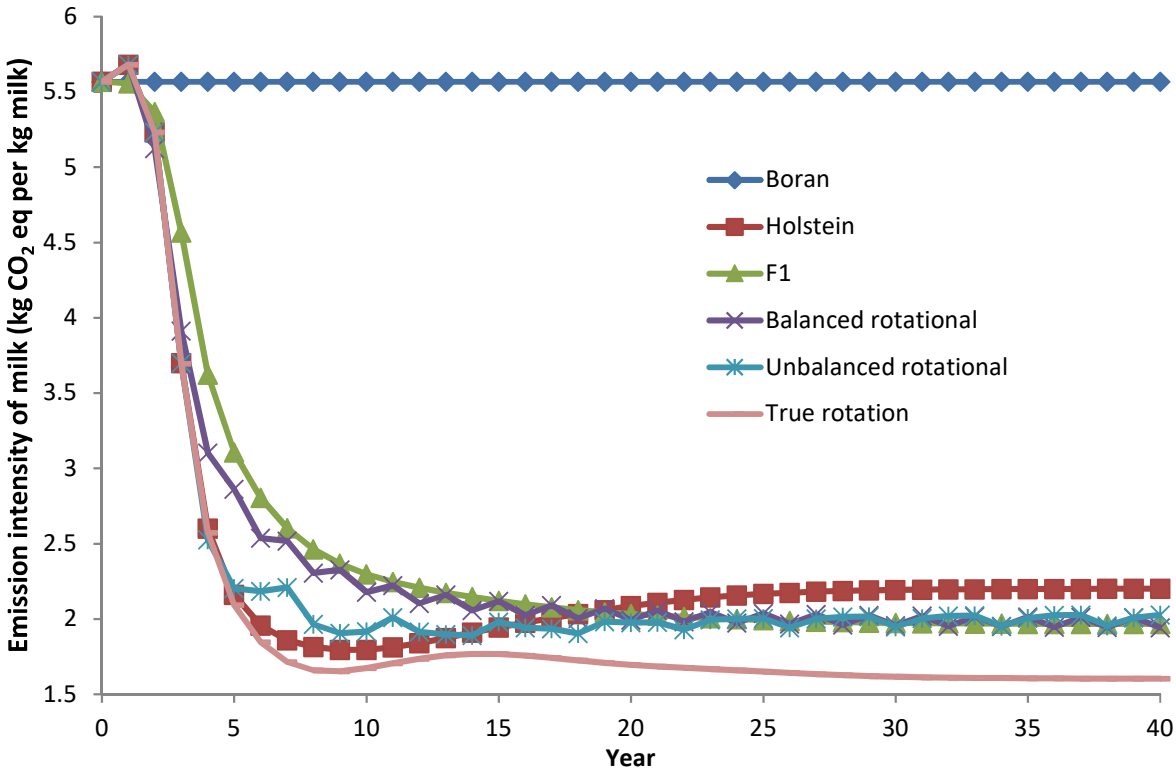
Figure 5.2. Total GHG emissions per cow in the herd from years 0-40 under the 5 strategies tested and compared to a baseline of a herd of purebred Boran.



5.3.3 Emission Intensity

Despite the predicted increases in GHG emissions per cow under all strategies tested, the models predicted a decrease in the emissions intensity of milk production over time compared to the initial level of the purebred Boran herd (5.57 kg CO_2 equivalents per kg FPCM) (see Figure 5.3 and Table 5.4). Other than the F1 sire strategy, there was a slight increase in emission intensity from year 0 to 1, corresponding to increased emissions of Holstein sired animals which were not yet producing milk. The Holstein sire and unbalanced and true rotational strategies led to the most rapid decreases in emission intensity, although by approximately year 25, all strategies except the true rotational led to very similar emission intensities. Overall, the true rotational strategy consistently performed the best, leading to the lowest average emission intensity across years 0-40 (2.03 kg CO_2 equivalents per kg FPCM produced) and a 3.5 fold reduction from the initial herd to year 40.

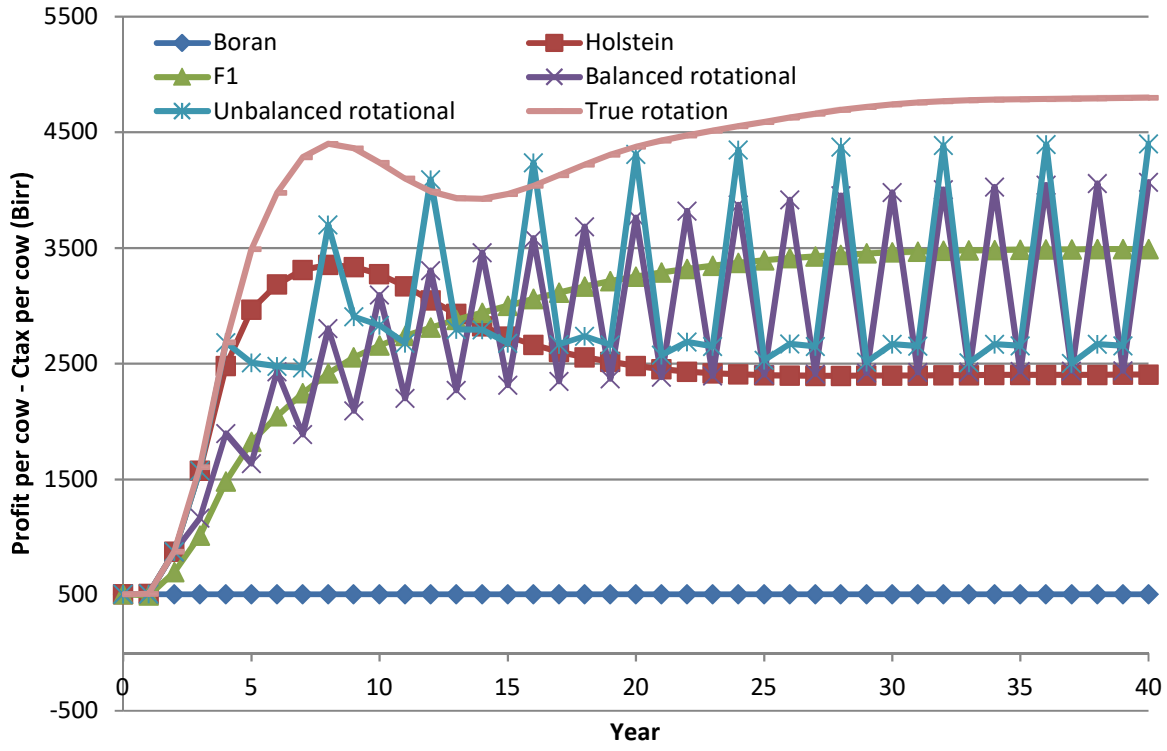
Figure 5.3. Emission intensity of milk (kg CO_2 equivalents per kg milk produced) from years 0-40 under the 5 strategies tested and compared to a baseline of a herd of purebred Boran.



5.3.4 Cost of Carbon

Annual profits after applying a carbon tax were less than those without a tax for all strategies, but broadly the ranking of strategies did not change (see Table 5.4 and Figure 5.4). The relative increases compared to the initial herd of Boran were much greater; for example the maximum annual profit per cow achieved in year 40 under the true rotational strategy was 9.5 times greater than that of the initial herd after applying a carbon tax, compared to only 3.9 times greater without the tax. Also, including a carbon tax resulted in the F1 sire strategy outperforming the unbalanced rotational strategy.

Figure 5.4. Annual profit - carbon tax per cow in the herd from years 0-40 under the 5 strategies tested and compared to a baseline of a herd of purebred Boran.



5.4 Discussion

In this study, a model to predict how varying crossbreeding strategies affect the profitability and GHG emissions of the herd was developed. The use of this model was illustrated to examine the effects of five crossbreeding strategies over 40 years on an initial herd of Boran cattle in Ethiopia.

5.4.1 Profitability

All strategies tested led to large increases in annual profit compared to the initial herd of Boran (up to nearly 4 times the initial annual profit under the true rotational strategy in year 40), driven primarily by the large increases in milk yield and so profits from milk sales due to the introduction of Holstein genes to the herd. As seen in the previous chapter, there is a

strong additive genetic effect for milk yield in this scenario and so, on average, increasing the proportion of Holstein genes in an individual tends to increase the milk yield. The sale value of surplus females and males also increased with increasing proportion of Holstein genes. However, there are also positive additive genetic effects for traits that affect predicted costs, in particular live weights for both yearling heifers and mature cows. Individuals with more Holstein genes tend to have greater weights and so have increased predicted feed costs. As seen in the previous chapter, the relative magnitude of increases in yearling weight is much smaller than the increases in milk yield in this crossing system and so despite increased costs, the increased income from milk is sufficiently large that all strategies led to increased profits compared to the initial herd of purebred Boran.

Crossbreeding also introduced non-additive genetic effects. In particular, heterosis was important for a range of traits that affected annual profits. Significant heterosis effects for a number of traits that affected annual costs were modelled. The positive heterosis for mature weight, yearling weight, lactation milk yield and milk fat content meant that strategies which lead to greater levels of heterosis had greater feed costs. However, the negative heterosis for health costs balanced this, meaning that heterosis level did not have a large effect on herd costs. Of the traits which were directly linked to income, only lactation milk yield had a significant heterosis effect modelled. The relative magnitude of this effect was one of the greatest (61% of the average of the purebred Boran and Holstein) and this was in line with the meta-analysis in Chapter 2 that showed milk production traits do tend to show the greatest heterosis in tropical cattle breeding (Bunning et al., 2019). This meant that strategies that increased the level of heterosis in the herd also greatly increased income due to milk sales and so overall, higher levels of heterosis tended to lead to higher profits. As in

the previous chapter, the strategies that led to high and consistent levels of heterosis across years 0-40 are the rotational strategies, particularly the true rotation.

A recombination loss effect was only modelled for lactation milk yield and mature weight and the relative size of this effect was much greater for milk yield compared to mature weight (-40% and -20% of the average of the purebred Boran and Holstein for lactation milk yield and mature weight respectively). For strategies with greater recombination, the negative effect of recombination on mature weight is beneficial as it reduces feed costs. However, because the effect on milk yield is relatively greater and milk yield has a large effect on income, the negative recombination loss for this trait means that strategies with greater recombination loss led to lower profits. Recombination loss expression in an individual is dependent on the level of crossbreeding in the parents (Dickerson, 1973) so that strategies that used a crossbred sire tended to lead to higher recombination loss levels across the herd compared to those that only use purebred sires. In particular, results of the previous chapter showed that the F1 sire strategy led to much higher levels of recombination across the herd and this may account for this strategy not leading to as high profits compared to other strategies that led to similar proportions of Holstein genes in the herd.

Another trait that has an indirect but important effect on profit is fertility. The fertility parameters used in this model are the age-specific calving rates for each crossbred type and are predicted using a genetic model of additive and non-additive effects for age at first calving (AFC) and calving interval (CI) and a deterministic fertility model (Chapter 3). Calving rates have an important effect on the composition of the herd, in terms of number of each animal type, which has an impact on profit. Firstly, when calving rates are high, more calves are produced per year which means there are more surplus animals which are sold for

income. Secondly, high annual calving rates reduce the number of dry cows in a year, which reduces the number of animals that have feed costs but no income from milk sales. Finally, higher calving rates reduce the number of replacements that are required to maintain the herd at a constant size and fewer replacements leads to reduced feed costs. In the Ethiopian Boran x Holstein case study, both AFC and CI have unfavourable additive Holstein breed effects, meaning that crossing strategies which increase the proportion of Holstein gene in the herd may lead to a reduction in calving rates. AFC and CI also have beneficial heterosis effects, meaning that strategies which increase the average heterosis expression in the herd will lead to an increase in calving rates. Therefore, strategies such as the true rotational strategy which increases the level of heterosis in the herd without increasing the proportion of Holstein genes too far led to high calving rates and so high profitability.

5.4.2 GHG Emissions

All strategies increased the GHG emissions per cow compared to that of the initial herd of purebred Boran. In the case study, many traits had unfavourable Holstein breed additive effects for reducing emissions, including mature weight, yearling weight and lactation milk yield. As all strategies increased the proportion of Holstein genes in the herd, all lead to increases in average mature weight, yearling weight and milk yields which led to an increase in predicted emissions per animal. It is worth noting that milk fat and protein percentages both had favourable Holstein breed additive effects for reducing emissions. However, the relative magnitudes of these effects and the impact of the traits on emissions were not sufficient to outweigh the unfavourable effect on lactation milk yield.

Heterosis effects for traits that affected predicted emissions were also unfavourable. Individuals with increased heterosis were predicted to weigh more and produce more milk

with greater fat and protein percentages, all of which increased the predicted annual GHG emissions per individual. Therefore, strategies that minimised increases in the average heterosis in the herd also minimised increases in predicted emissions. Conversely, for the two traits where recombination loss was modelled (mature weight and lactation milk yield), increased recombination loss was favourable for reducing GHG emissions. Strategies where a crossbred sire was used led to increased recombination loss across the herd and so reduced GHG emissions.

As for profitability, the fertility of cows in the herd had an important impact on GHG emissions. A herd with a greater calving rate will have more pregnant cows, calves born and lactating cows leading to greater GHG emissions. However, a greater calving rate also reduces the number of replacements that are required to maintain the herd at a constant size and so strategies that increase calving rates will also reduce GHG emissions from rearing replacements, but this is not sufficient to outweigh the increases from other animal types. Calving rate and therefore associated GHG emissions were minimized by crossing strategies that minimized heterosis whilst maximizing increases in Holstein genes and recombination loss.

5.4.3 Emission Intensity

Emissions intensity (EI) is considered a good metric for measuring both production and GHG emissions simultaneously and by reducing EI we can reduce emissions whilst maintaining a consistent level of production. In this case, the kilograms of CO_2 equivalents per kilogram of milk produced was considered, in order to reduce GHG emissions whilst maintaining the level of food production and a major income source.

Increasing milk yield per cow is considered a good way to reduce EI as this increases the amount of milk produced at a faster rate than the emissions increase (Gerber et al., 2013). If we simply considered the additive Holstein breed effect of milk yield, we might expect the Holstein sire strategy to minimize EI. However, as the results of the previous chapter show, when we also consider non-additive genetic effects for milk yield alongside the effect of fertility on herd composition, the true rotational strategy performs best for maximising annual milk yield per cow. This explains the low EI under this strategy and why it outperforms all other strategies tested (resulting in a 3.5 fold reduction in annual EI from the initial herd to year 40).

FAO (2017) report that the average EI of milk production in Ethiopia is 24.5 kg CO_2 eq./kg FPCM across all farming systems, which is much greater than any of the estimates produced in this thesis. However, this estimate includes pastoral and agro-pastoral systems which are much less efficient and have EIs of 44.6 kg CO_2 eq./kg FPCM. The same study reports emission intensities of 8.7 and 3.8 kg CO_2 eq./kg FPCM for Ethiopian small and medium scale commercial systems respectively, which are closer to those predicted here and also a more similar production system. These estimates use the Global Livestock Environmental Assessment Model (GLEAM) (Gerber et al., 2013) which as well as considering enteric methane and emissions from manure, also considers emissions from feed production which were not included in this work. Therefore, this may account for the smaller predicted EIs from models described in this thesis, compared to those reported for small-scale production systems. If emissions due to feed production had been included, the ranking of the strategies is unlikely to have changed as traits affecting enteric and manure emissions also affect feed requirements. However, as well as increasing all predicted EIs, including other emissions sources may have increased the differences between the strategies.

In our model, we have considered the emission intensity of milk. As described in chapter 1, there are other varying methods which could have been used. These allocate emissions to either main products, for example milk or meat, or to a wider range of uses, including draught power, manure and as a capital asset (Opio et al., 2013; Weiler et al., 2014).

5.4.4 Cost of Carbon

A limitation of the EI of milk metric is that it is measured in a unit which has little meaning for a typical farmer. An alternative strategy to combine profitability and GHG emissions is to apply a form of carbon tax, which can then be included as a cost in the profitability model. Broadly, the ranking of strategies for annual profits after a carbon tax does not change because the differences between strategies are much greater for profitability than for GHG emissions. However, after including a carbon tax, the F1 sire strategy outperformed the unbalanced rotational strategy, due to the previously discussed low GHG emissions under the F1 sire strategy.

As this method includes an additional cost to herds, annual profit with a carbon tax was less than without a tax for all strategies. The introduction of this tax to smallholder farmers in Ethiopia is therefore unrealistic and results show that a tax of about 30USD would have little effect on the ranking of crossing strategies. However, they do highlight the potential to financially incentivise the use of F1 sires to reduce GHG emissions and this could potentially be achieved through a subsidy rather than tax system.

5.4.5 Model limitations

This model estimates net energy requirements using calculations suggested in the IPCC tier II framework, originally derived for cattle in the USA (CSIRO, 2007). Both the environmental conditions and genotypes of the cattle modelled here are significantly different to those

used to derive these calculations. In hot climates in SSA, cattle may require additional energy to dissipate body heat, which would increase the maintenance energy requirements (CSIRO, 2007), leading to increased feed requirements. The feed quality is also likely to be poorer in SSA than the USA. More fibrous feeds are associated with increased energy requirements for chewing and digestion (Goetsch et al., 1997), which would again increase feed requirements. Increases in feed requirements would result in reduced predicted profit and increased predicted GHG emissions. As we are considering breeding strategies, variation in the fit of the energy models across genotypes could have a significant effect on the reliability of results. Differences have been found in between breeds of sheep and it is suggested that tropical breeds tend to have higher growth energy requirements as they have not been selected for muscle deposition (Early et al., 2001). However a meta analysis of nutritional requirements of cattle in warm climates did not find a significant effect of genotype on estimates of maintenance or growth energy requirements calculation (Salah et al., 2014).

A single feed cost per nutritional requirement was used across our models. In reality, feed costs are likely to vary, both according to feed type as well as seasonal and yearly conditions. Crossbreds with more exotic genetics are likely to require higher quality feed (Tahir et al., 2018); although this would have a higher digestible energy per kg of dry matter (e.g. 10.5 MJ of ME for maize silage (Chakeredza et al., 2008), compared to 7.1 MJ used for our case study), it would also be significantly more expensive than that modelled here (e.g up 4.17 Birr per kg for Wheat bran (Bediye et al., 2018), compared to 0.7 Birr per kg in our case study). Although more expensive, an animal will require less of these high energy feeds, potentially offsetting the cost. Feed is also likely to vary over time, for example, one study showed that on average a dairy ration in Ethiopia increased in cost by 83% from 2010/11 to 2015/16 (Bediye et al., 2018). The authors suggested this was due to shortages of, and

therefore high prices of, feed ingredients. For farms near urban areas, feed may have to be transported, increasing the cost. However milk prices for these farmers are also likely to be higher (e.g. 12-15 Birr per L (Diriba et al., 2014), compared to 5.1 Birr per kg in our case study). Indeed, we might expect milk prices to be higher in general when feed prices are high, which would offset the higher costs. However, if feed costs increase disproportionately, strategies which increase the proportion of exotic genetics would be less favourable than our results show, as increases in animal size will increase feed requirements. The use of more detailed feed and cost information in modelling would increase the reliability of the results.

5.4.6 Optimal Strategy

To maximise profitability, the true rotational strategy was best - this maximises heterosis, minimises recombination loss and results in intermediate levels of Holstein genes. This strategy uses purebred sires to maximise heterosis and minimise recombination loss, resulting in high milk yields and moderate sale animal value with moderate feed costs and moderate to low health costs, as well as high fertility. However, this same strategy led to some of the highest predicted average annual GHG emissions per cow (after the Holstein sire strategy).

To minimise GHG emissions, strategies such as the F1 sire which minimise increases in the proportion of Holstein genes whilst maximising recombination loss and minimising heterosis are best. The F1 sire strategy uses crossbred sires to maximise recombination loss and results in intermediate heterosis and the lowest average annual proportion of Holstein genes of any of the five strategies tested, leading to low weights and milk yields and

therefore low emissions. However, this strategy was one of the poorest at increasing annual profits, mainly due to the low milk yields.

When considering the whole timescale modelled, the Holstein sire strategy performed the worst for both profitability and GHG emissions, having the lowest average annual profit per cow and the highest average annual GHG emissions per cow of all 5 strategies tested. This is because it results in the majority of the herd having a very high proportion of Holstein genes. These animals do not produce much more milk nor milk sales income than individuals with intermediate levels of Holstein genes, and they weigh more, which leads to higher feed costs. This is the cause of the drop in annual profits after year 8. The strategy also performs poorly when considering GHG emissions, again due to the heavier animals produced due to the high proportion of Holstein genes. These results highlight the importance of considering long-term responses to crossing strategies. Whilst herd performance and profitability under the Holstein sire strategy were high in the first few years due to the production of many F1s, the drop in performance predicted after year 8 results led to the low average annual profits when considering years 0-40. These long-term results also highlight the problems with grading up strategies, particularly those resulting in very high proportion exotic genetics. Grading up strategies are commonly implemented across the tropics and although they perform well in the first generation, performance of subsequent generations is highly variable between systems (Cunningham and Syrstad, 1987; Galukande et al., 2013).

When selecting an optimal strategy, the practicalities of implementation must also be considered. Of the five tested here, the F1 strategy would be the simplest because the same sire type is used every year and importantly, sires could be used via natural service. Although the Holstein sire strategy also uses the same sire type every year, matings would need to be via artificial insemination (AI). AI is increasingly available in parts of Ethiopia (Guadu and

Abebaw, 2016) but success rates are low (Juneyid et al., 2017) and therefore without improving the availability and success of AI, strategies that use Holstein bulls may be less successful than predicted by these models. The balanced and unbalanced rotational strategies are slightly more complex to implement as they reply of the use of different sire types across years, but all females are still mated to the same sire within a year and these strategies have some years where natural service can be used. Although the true rotational strategy led to greatest predicted profit, it is the most complex to implement as not all females are mated to the same sire in a year. It also requires some basic record keeping (sire of each female to be known) so that farmer can know which bull type to use. These practical issues may mean that also this strategy led to the greatest predicted profit, farmers may prefer to use a different strategy.

For farmers that are primarily concerned with maximising profitability, from the five strategies tested here, they are most likely to select the true rotational strategy. Results from this chapter show implementing this strategy would increase profits 3.4 fold compared to a herd of the local breed and this is because this strategy maintains an intermediate proportion of Holstein genes whilst maximising heterosis. Unfortunately, this strategy also increases gross GHG emissions by 33% compared to the initial Boran herd, assuming the herd size remained constant. However, as the aim is to increase production whilst mitigating GHG emissions, EI rather than total emissions was considered and the true rotational strategy would also lead to the greatest reduction of milk EI among all strategies tested, allowing either increased milk production for the same GHG emission level, or the maintenance of milk production by keeping fewer cows and reducing GHG emissions. Including a carbon tax into the profitability model did not affect the best crossing strategy, but it did increase the amount by which this best strategy is superior over the initial herd of

Boran (8-fold increase in annual profit per cow), again suggesting that when both emissions and economics are considered, the true rotational is the optimal strategy. These results show the power of heterosis to increase production and profitability of a herd and highlight the potential of a systematic crossing strategy to maximise heterosis.

Chapter 6: Crossbreeding cattle in sub-Saharan Africa: Testing scenarios and strategies

6.1 Introduction

In previous chapters we have described our models to test crossbreeding strategies for cattle in sub-Saharan Africa and used the model to test a limited number of strategies for an Ethiopian farming system as an exemplar, introducing Holstein genes to the local Boran breed. From results for strategies tested in previous chapters, we know that simple grading up strategies are not the best for maximising long-term profits or mitigating GHG emissions.

Of the strategies tested in the previous chapter, the true rotation strategy (TR), where sire type was alternated between Holstein and Boran each generation, resulted in the highest average annual profit and lowest GHG EI of milk. Rotational breeding strategies can be favoured by farmers as they produce individuals with intermediate levels of desirable traits from both breeds (Cunningham and Syrstad, 1987) and also because they lead to high levels of heterosis which is usually beneficial (Bunning et al., 2019). As TR performed well in our case study system, we designed two additional similar rotational strategies where sire type is changed according to generation to take advantage of favourable heterosis. The first, delayed true rotation (DTR), uses a Holstein sire for the first two generations and then sire type is alternated between Boran and Holstein every generation. We expect this strategy to perform similarly to the true rotation strategy (TR), but with the potential to reduce the drop in profit seen under the true rotation strategy after the initial peak. The second new breeding strategy is the unbalanced true rotation (UTR) where a Holstein sire is used for two generations, followed by one generation where a Boran sire is used and this pattern

repeated. This strategy is expected to lead to lower heterosis levels compared to TR and DTR but slightly higher average proportion of Holstein genes.

Although TR led to high profitability, the practicalities of implementing this strategy may be more complex than some others. TR uses a Holstein sire for 50% of matings and Holstein sires are unlikely to be used via natural service in sub-Saharan Africa. Artificial insemination (AI) in Ethiopia has low success rates (Juneyid et al., 2017) and is only available in certain areas (Guadu and Abebaw, 2016). Therefore, strategies that minimize the use of AI may be more likely to be successful. The formation of composites is a crossbreeding strategy that relies less on the use of purebred sires. A composite, sometimes known as a synthetic breed, is formed by crossing two (or more) breeds to form crossbreds that are then mated together, rather than relying on sires from the parental breeds (Simm, 2000). Composites have many of the advantages of other crossbreeding strategies; they allow breeders to take advantage of complementary traits from multiple breeds, for example tropical adaptation from a zebu breed with milk production from Holsteins, and composites retain some, but not the maximum heterosis of other crossbreeding strategies (Cunningham and Syrstad, 1987; Kebede et al., 2018). However, the performance of individuals does not vary from generation to generation in the same way as rotational strategies. Also, so long as a large enough population is maintained to minimize inbreeding, composite breeds do not require the continued use of bulls of other breeds, minimizing the need for AI and also potentially allowing selection of sires within the same production system. We designed a composite strategy which limits the use of purebred sires and takes advantage of the benefits of both local and exotic breeds. This strategy creates a 50:50 composite by initially crossing all Boran females to Holstein sires, producing F1s, which are then bred to F1 sires from this generation onwards.

All strategies tested described so far involve crossbreeding within the herd. We know from results of the previous chapters and other studies (McDowell et al., 1996; Rutledge, 2001) that F1 individuals result in the highest profitability and lowest milk emission intensity, mainly due to their high milk yield due to the maximum expression of heterosis, whilst only intermediate size and therefore feed costs. However, a herd of F1 individuals is not able to sustain itself as F1s must be bred from two purebred parents and mating of F1s (as in the composite strategy described above) results in the formation of F2s which express much less heterosis and more undesirable recombination loss (Rutledge, 2001). It may be possible for a farmer to sell all calves born from their F1 herd and buy in F1 replacement heifers from elsewhere. Therefore, we test this final strategy by modelling the performance of a herd of F1s, including the additional costs of buying in all replacements.

So far, all strategies have been tested under a single scenario which, although representative of a common Ethiopian system, does not model any genetic variation in cow survival. Variation in the survival of different types of crossbreds is an important factor in the determination of an optimal crossing strategy as it determines the number of replacement heifers needed to be reared. For all results so far, although genetic variation in fertility (which also affects replacement rate) was modelled, genetic variation in survival was not. This was due to lack of data for survival or traits related to survival.

However, we know that there is likely to be genetic variation in survival. We would expect an additive breed effect, with crossbreds with a higher proportion of exotic genes not being as well adapted to tropical conditions, and therefore having lower survival. Other studies have shown problems with the survival of exotic or crossbreds with high proportion of exotic genes. One review found that breeding programs across the tropics did not favour 75% exotic crossbreds because although they had the potential to produce slightly more milk,

they had high mortality rates (Mcdowell, 1985). Another review found that the average rate of death and culling for adult cows increased from 14.8% for animals with 0-25% exotic genes, to 18% for purebred exotics (Vaccaro, 1990). A study of Holstein-Friesian heifers in Kenya found high mortality and culling rates but that heifers sired by bulls originating from South Africa and Israel, rather than temperate regions, tended to have higher survival rates (Menjo et al., 2009), suggesting that low survival rates may be due to the selection of bulls that are not adapted for local conditions, including high heat, food or water shortages or disease pressures. The magnitude of the additive effect for survival is likely to vary depending on the pressures of the system. Therefore, we tested the effect of including a range of sizes of additive effect for cow survival.

Survival rates of cattle with exotic genes can be poor for a variety of reasons. Firstly, these animals require a higher quantity or quality of feed. In situations where this is not possible, this can negatively affect survival of crossbred cattle, as discussed by Ghulam Habib et al. (2016) for similar local x exotic cattle in Pakistan. The survival of temperate breeds of cattle is also more likely to be affected by droughts. In a study of beef cattle in Australia, during a drought, mortality rates for the temperate breeds were significantly higher than for tropical x temperate crossbreds (Frisch, 1973). The frequency of extreme weather events such as droughts that result in water and feed shortages are likely to increase in the future due to climate change (Stott, 2016) and so the importance of considering breed adaptation to survival in these conditions will become increasingly important. As well as climate adaptation, lack of parasite and disease tolerance is the likely cause of reduced survival of exotics. In areas of Africa where certain diseases are endemic, local cattle breeds are tolerant or resistant to the disease, allowing them to survive, whereas exotic breeds would either not survive or require veterinary intervention to survive. This is the case for areas of

West Africa where the presence of trypanosomiasis and the extreme mortality of non-adapted breeds means that exotics and crossbreds are not kept (Kim et al., 2017). Similarly in areas of eastern, central and southern Africa where East Coast Fever is common, some local breeds show resistance either to the disease or to the ticks which transmit the disease (Vajana et al., 2018).

In addition to an additive genetic effect, genetic variation in survival of crossbreds is also likely to be due to a heterosis effect for this trait. From results of our meta-analysis of heterosis in tropical cattle breeding, we know that longevity traits tend to show high, positive heterosis (+35% of the mean purebred performance) from the results of chapter 2. A study of temperate beef breeds found significantly more crossbreds than purebreds remained in the herd to 12 years of age (42% vs 25%) (Núñez-Dominguez et al., 1991), suggesting the expression of a heterosis effect for this trait. We therefore also tested the performance of varying crossbreeding strategies under scenarios with varying magnitudes of positive heterosis for cow survival.

Varying the genetic background for survival will change the predicted profits and GHG emissions of crossbreeding strategies, but what is of most concern to a farmer, are scenarios where the ranking of strategies changes. In particular, we are interested in finding situations where conditions are so poor for animals with a high proportion of Holstein genes that despite potential increases in milk production, profits of the initial herd of purebred Boran are greater than other strategies.

The first aim of this chapter is to refine the optimal strategy for the Ethiopian case study, by testing two refined rotational strategies, a simpler-to-implement composite strategy and a strategy where the optimal crossbred replacements are bought in, rather than being bred. The second aim of this chapter is to test all strategies under scenarios with varying additive

and non-additive genetic variation for survival, identifying under what circumstances the optimal strategy is likely to change.

6.2 Materials and Methods

To test a range of further strategies and scenarios, the fertility, genetic, herd and economic models described in previous chapters were used. Again, although this model is applicable for a range of systems across SSA, a case study of smallholder cattle farming in the Oromiya region of Ethiopia was considered as an exemplar as we have good data on this system. The initial herd is made up of local Boran cattle and sires used were either Boran, Holstein or an F1 (a crossbred from a Boran dam, sired by a Holstein).

6.2.1 Additional Rotational Breeding Strategies

As with the true rotational strategy (TR) described in previous chapters, two additional strategies tested here also varied sire type between a Boran or Holstein sire depending on the pedigree of the cow. In the previously described TR, cows sired by a Boran were bred to a Holstein bull whereas cows sired by a Holstein were bred to a Boran, resulting in alternating sire types each generation. We also tested a delayed true rotational strategy (DTR) where the same rules as in TR were followed except that F1 individuals were also bred to a Holstein sire, resulting in the first two generations being sired by a Holstein, then a rotation between sire types for each subsequent generation. Finally, we tested an unbalanced true rotational strategy (UTR) where cows were bred to Holstein sires unless both their sire and paternal grandsire had been Holsteins, in which case they were bred to Boran sires, resulting in a Holstein sire being used for two generations, followed by one generation where a Boran sire is used. This pattern is then repeated.

These rules were used as inputs for the models, along with all previously described input parameters for the Ethiopian case study and annual profit per cow, GHG emissions per cow, milk emissions intensity (measured in kg CO2 equivalents per kg fat and protein corrected milk (FPCM) were predicted from year 0-40.

6.2.2 Composite strategy

Under this strategy the sire type used depended on the pedigree of the cow. Purebred Borans were bred to Holstein sires whilst all other crossbred types were bred to F1 sires. Again, this strategy was used as an input for the models, along with all previously described input parameters for the Ethiopian case study and annual profit per cow, GHG emissions per cow, milk emissions intensity (measured in kg CO2 equivalents per kg fat and protein corrected milk (FPCM) were predicted from year 0-40.

6.2.3 Buy in F1 replacements

To test this strategy, the economic and herd composition models had to be altered. Rather than modelling an initial herd of purebred Borans, the initial herd composition was changed to all F1s. Replacement rates were set to zero for all crossbred types, meaning that all calves born became surplus males and females. Sires used for all crossbred types and across all years were F1s as these would produce more valuable calves whilst being more practical for farmers than Holstein sires.

A constant number of F1 yearlings were introduced into the herd composition every year, which were equal to the number required to maintain the herd at a constant size, calculated using the replacement rate of F1s and number of calves born each year. The additional cost of buying in these F1s yearlings was estimated in the same way that the sale value of surplus F1 yearling heifers was calculated in our economic model and was added in as an additional

annual cost to the economic model. After making these changes, the annual profit per cow, GHG emissions per cow, milk emissions intensity (measured in kg CO2 equivalents per kg fat and protein corrected milk (FPCM) were predicted. These would remain constant so did not require modelling over any time period.

6.2.4 Varying Survival

In previous chapters, a constant annual death rate of 0.24 was used across all ages and crossbred types of adult cows. To investigate the effect of varying this, a genetic model was used to produce varying death rates for each crossbred type.

$$\mathrm{Death_C} = \mathrm{al_C}\,\mathrm{L_{Death}} + \mathrm{ae_C}\mathrm{E}_{Deat} + h_C H_{Death}$$

Where $\mathrm{Death_C}$ is the probability that a cow (>1 year old) of crossbred type C leaves the herd from one year to the next and is calculated using a genetic crossbreeding model (Dickerson, 1973) which considers the local and exotic breed means and heterosis effects (L, E and H respectively) for the trait for crosses of the specific pair of breeds and in a specific system, which are then weighted (al, ae and h) depending on the crossbred type. The 18 potential crossbred types and their associated weights for the genetic model ($\mathrm{al_C}$, $\mathrm{ae_C}$ and $\mathrm{h_C}$) are defined in previous chapters (see table 5.2). For our case study, L refers to the Boran breed and E to the Holstein breed. Therefore a value of 0.24 was used for $\mathrm{L_{Death}}$ as the mean annual death rate of a purebred Boran cow. $\mathrm{E_{Death}}$, the mean annual death rate of a purebred Holstein cow and $\mathrm{H_{Death}}$, the maximum heterosis for cow annual death rate, have previously been equal to $\mathrm{L_{Death}}$ and 0 respectively, resulting in no genetic variation for this trait.

In order to introduce an additive effect for death, we varied $\mathrm{E_{Death}}$. Holsteins are expected to have a higher death rate than the locally adapted Borans and so we tested scenarios where $\mathrm{E_{Death}}$ was 20%, 50% or 80% higher than $\mathrm{L_{Death}}$, resulting in values of 0.29, 0.36 or 0.43. In

order to introduce a heterosis effect for death, we varied H_{Death}. Heterosis is expected to be negative for death rate as it is usually positive for longevity traits (from results of Chapter 2), so we tested scenarios where H_{Death} was negative and 20%, 50% or 80% of L_{Death}, resulting in values of -0.05, -0.12 and -0.19. We then tested all previously tested crossbreeding strategies, including those introduced in this and previous chapters, under these scenarios and compared average annual profits per cow from years 0-40.

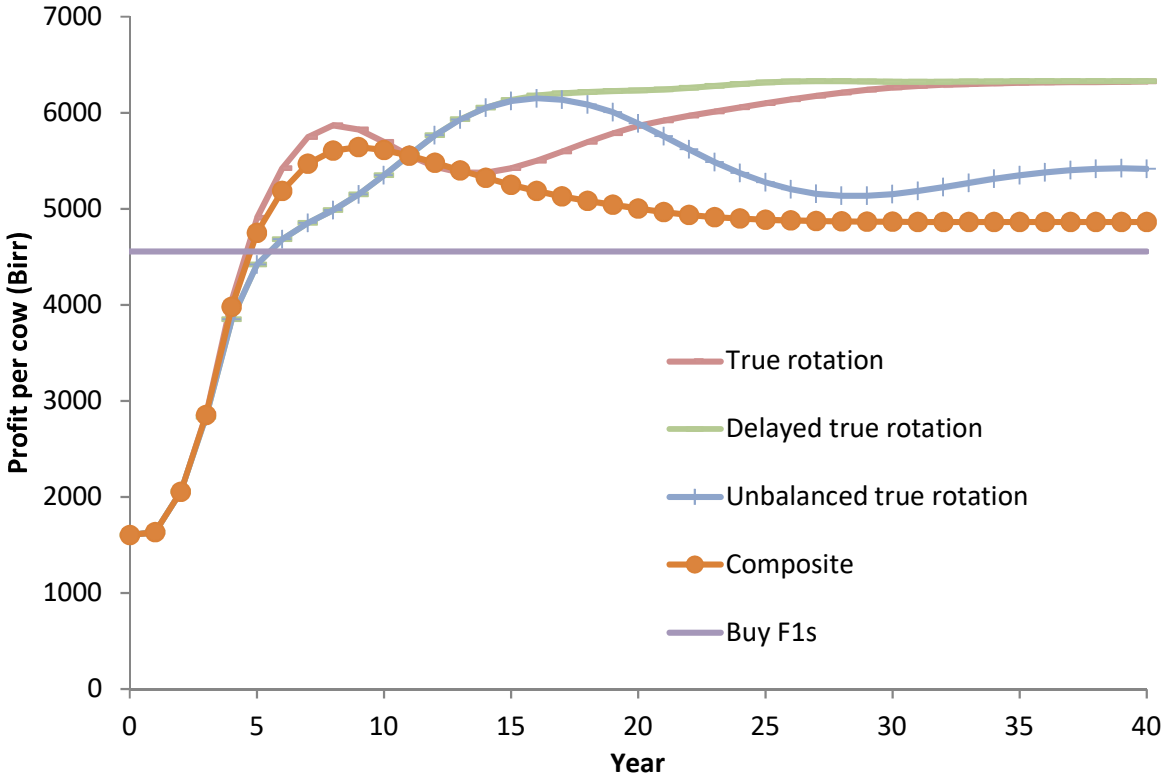
In order to find scenarios where the ranking of different breeding strategies changes significantly, we varied E_{Death} systematically, first searching for the threshold where the Holstein sire strategy resulted in lower average profit per cow over years 0-40 than annual profits of the initial Boran herd. This was repeated for 0, 20, 50 and 80% heterosis. Secondly, we searched for the threshold of E_{Death} where annual profits per cow for the initial herd of purebred Boran were greater than the average annual profits per cow from years 0-40 of any of the crossbreeding strategies.

6.3 Results

6.3.1 New strategies

6.3.1.1 Profitability

Figure 6.1. Annual profit per cow in Ethiopian Birr from years 0-40 under the previously tested true rotation strategy, the two new specific sire strategies, the composite strategy and the strategy where F1 replacements are bought in annually.



None of the new breeding strategies led to higher annual profits per cow in years 0-11 than those under TR, which peaked at 5869 Birr in year 8 (see Figure 6.1). The composite strategy led to similar, but slightly lower annual profits during this period, peaking at 5642 Birr in year 9. Both new rotational strategies (DTR and UTR) led to lower annual profits during this period. However during years 12-16 the decline in annual profits of the TR and composite combined with the increases for both new rotational strategies led to these new rotational strategies having the highest annual profits. From year 16 onwards, predicted annual profits

under UTR decreased compared to that of DTR, meaning that for this period DTR led to higher annual profits than all others. Predicted profits under TR increased during this time so that by year 35, both TR and DTR had similarly high predicted annual profits (about 6300 Birr per cow). Compared to TR, the composite strategy had lower predicted profits from year 15 onwards due to the continued decline and then flattening of annual profits, reaching 4862 Birr per cow in year 40. When considering the average annual profits across years 0-40, DTR performed best and the composite the worst of all breeding strategies (Table 6.1).

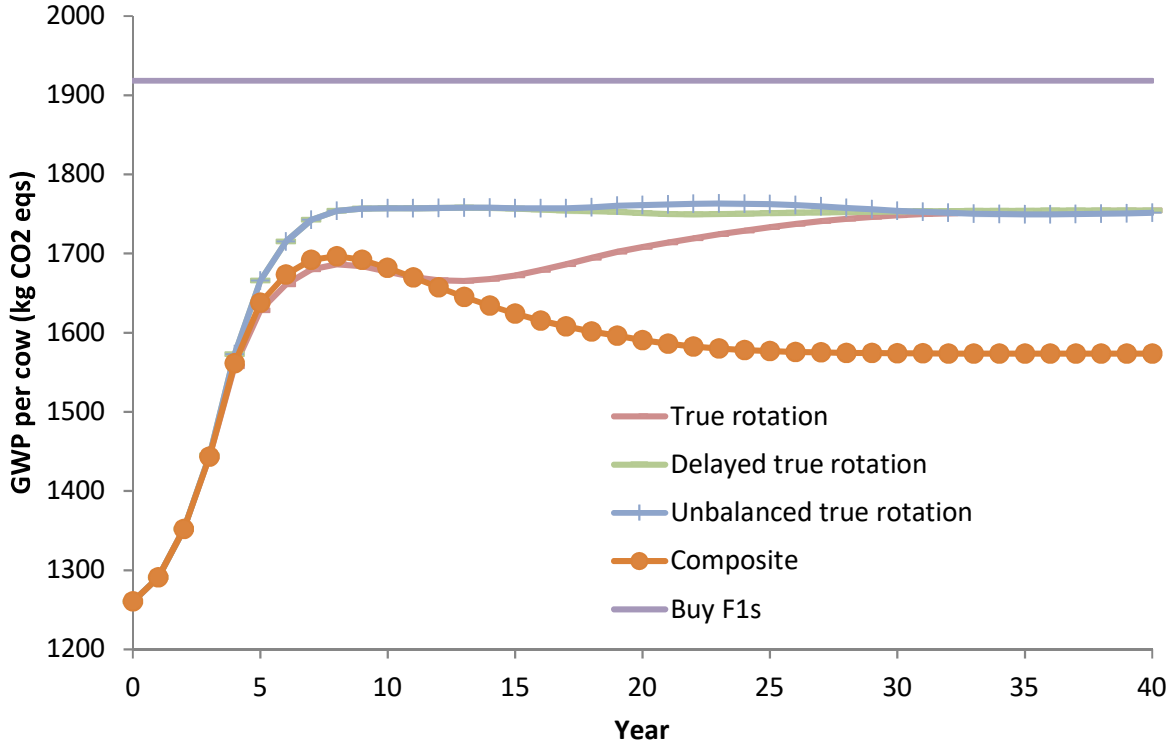
As expected, the buying F1 strategy led to a constant predicted annual profit (4555 Birr per cow). Initially, from years 0-4, this was higher than that predicted under any of the breeding strategies tested. However from year 6 onwards, all breeding strategies led to higher annual profits than the buying F1 strategy and when we consider the average across years 0-40, this strategy led to the lowest profits (Table 6.1).

Table 6.1. Annual profit per cow, global warming potential (GWP) per cow and emission intensity (EI) of fat and protein corrected milk (FPCM) for the initial herd of purebred Boran and under the previously tested true rotation strategy, the two new rotational strategies, the composite strategy and the strategy where F1 replacements are bought in annually. Numbers in brackets show the rankings of each strategy for that metric with 1 being the best and 5 the worst.

Strategy	Annual profit per cow (Birr)	GWP per cow (kg CO_2 equivalents)	EI of milk (kg CO_2 per kg FPCM)
Boran herd	1604	1260	5.57
True rotation	5499 (2)	1673 (2)	2.03 (3)
Delayed true rotation	5567 (1)	1705 (3)	2.02 (2)
Unbalanced true rotation	5069 (3)	1707 (4)	2.11 (4)
Composite	4742 (4)	1579 (1)	2.21 (5)
Buy F1s	4555 (5)	1918 (5)	1.35 (1)

6.3.1.2 GHG EMISSIONS

Figure 6.2. Annual greenhouse gas (GHG) emissions per cow in kgs of CO_2 equivalents from years 0-40 under the previously tested true rotation strategy, the two new specific sire strategies, the composite strategy and the strategy where F1 replacements are bought in annually.

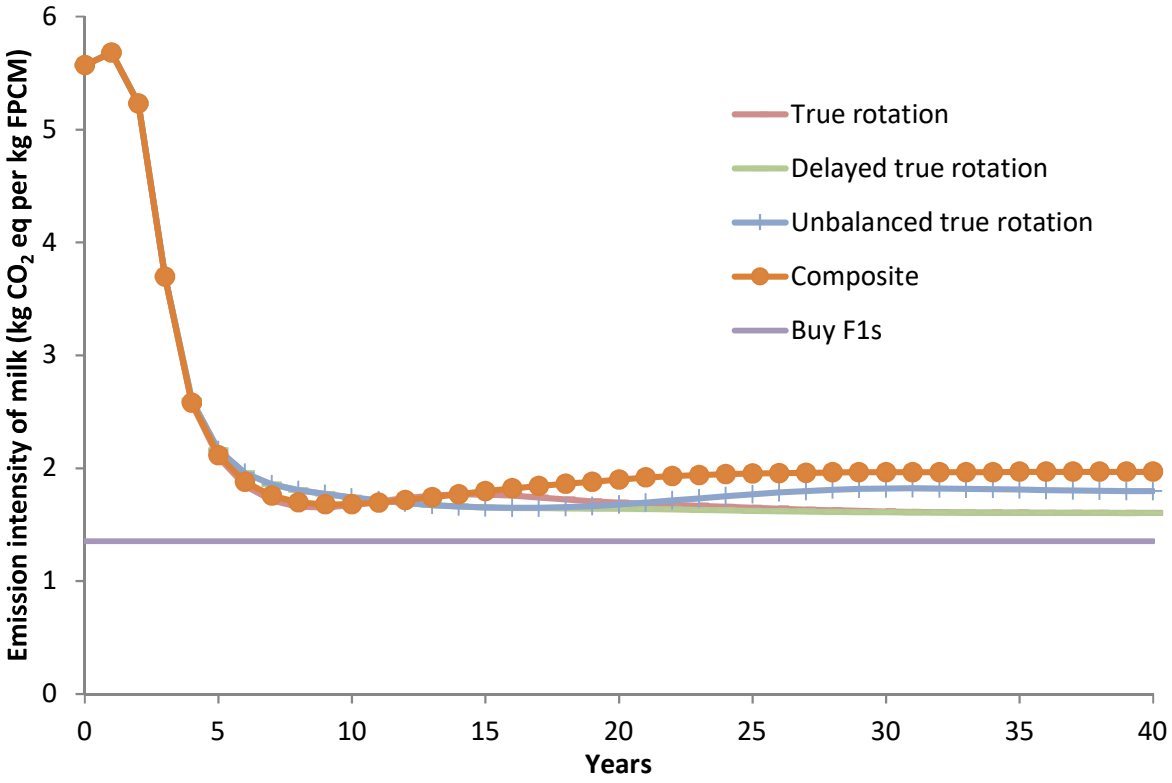


As expected from the results of the previous chapter, all strategies led to increases in annual GHG emissions per cow compared to the initial value of 1260 kg CO_2 eq (Figure 6.2). The composite strategy tended to lead to the lowest annual emissions, peaking at 1697 kg kg CO_2 eq. per cow in year 8 but then decreasing again, reaching 1574 kg CO_2 eq. per cow in year 40. The new rotational strategies (DTR and UTR) led to the highest annual emissions of any of the breeding strategies, increasing quickly from years 0-10 and then stabilising at around 1750 kg CO_2 eq. per cow, per year for the remaining years. Predicted emissions of TR initially followed those predicted under the composite strategy, but then increased from year 12,

reaching the same level as emissions predicted for the other rotational strategies by year 31. The buying F1s strategy led to higher predicted annual emissions (1918 kg CO_2 eq. per cow) than any of the breeding strategies tested in every year. On average, across years 0-40, the composite strategy led to the lowest annual GHG emissions per cow (1549 kg CO_2 eq.) (Table 6.1).

6.3.1.3 Milk Emission Intensities

Figure 6.3. Annual emission intensity of milk, measured in kg CO_2 equivalents per kg fat and protein corrected milk (FPCM), from years 0-40 under the previously tested true rotation strategy, the two new specific sire strategies, the composite strategy and the strategy where F1 replacements are bought in annually.

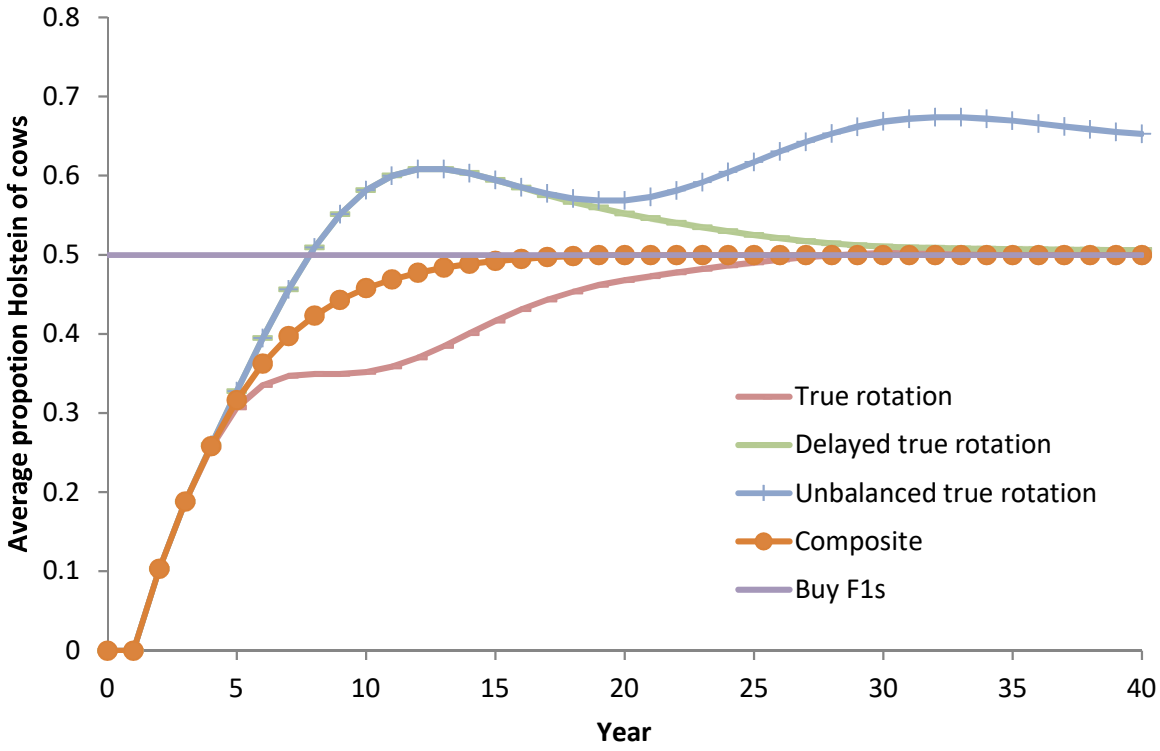


All new breeding strategies resulted in similar changes in milk emission intensities across years 0-40, increasing slightly in year 1 from 5.57 to 5.68 kg CO_2 eq. per kg FPCM, followed by a steep decline and levelling off from years 2-8, reaching around 1.7 kg CO_2 eq. per kg FPCM (Figure 6.3). On average over years 0-40, DTR led to the lowest and the composite strategy to the highest milk emission intensities of the breeding strategies tested here (Table 6.1). Despite the low profits and high emissions per cow, the buying F1s strategy led to even lower milk emission intensity (1.35 kg CO_2 eq. per kg FPCM), although it is worth noting that this value does not account for the greater emissions produced off-farm under this strategy.

6.3.1.4 GENETIC EFFECTS

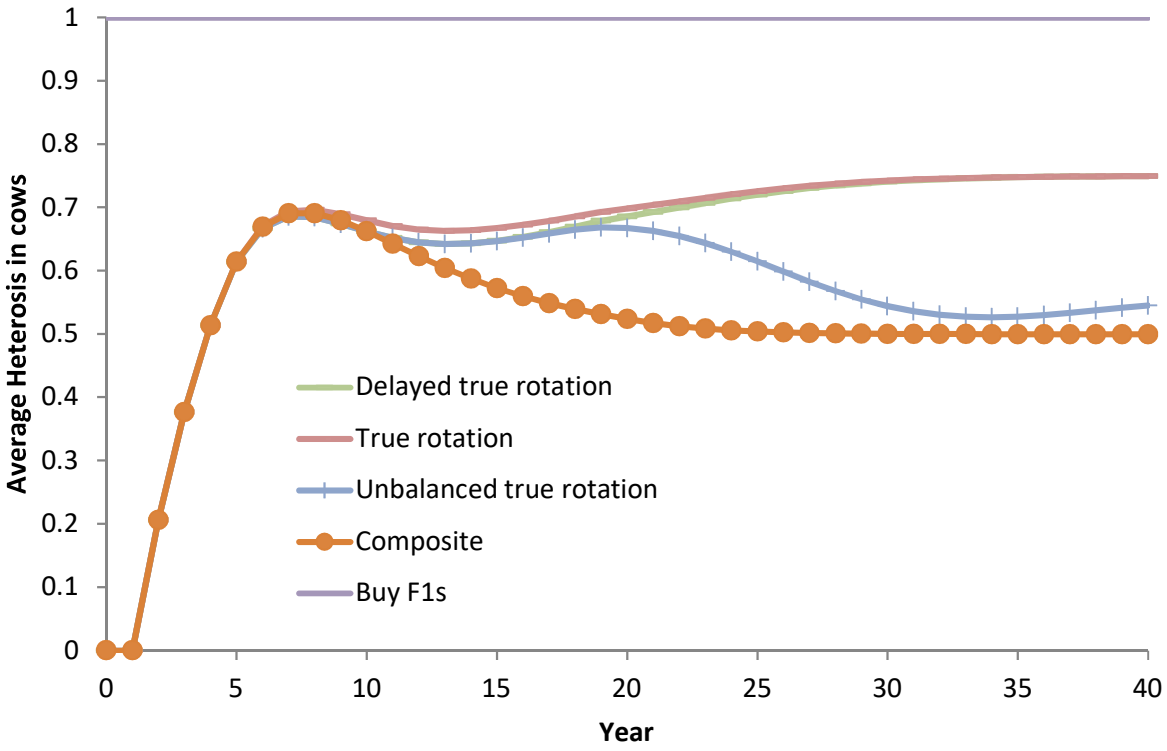
Both the new rotational strategies (DTR and UTR) led to a greater rate of increase of Holstein genes in the herd from years 0-12, peaking at 60% in year 12 and then decreasing slightly (Figure 6.4). However from year 19, DTR led to a greater decrease in Holstein genes, converging along with TR and the composite strategy at 50% by year 30. From year 19, UTR led to an increase in Holstein genes again, up to a maximum of 67%. The proportion of Holstein genes in the herd under the composite strategy increased quickly at first but this rate decreased over time until 50% Holstein genes was reached in year 17, after which no change was seen. TR led to the slowest increase in Holstein genes, initially increasing at the same rate as other strategies but from years 7-10 very little change was predicted. After this, it increased again, reaching a maximum of 50% by year 27.

Figure 6.4. Annual average proportion of Holstein genes in cows, from years 0-40 under the previously tested true rotation strategy, the two new specific sire strategies, the composite strategy and the strategy where F1 replacements are bought in annually.



Under all breeding strategies tested, average heterosis in adult cows increased from 0 in year 1 to 0.69 in year 8 (Figure 6.5). Under the composite strategy, heterosis decreased at the fastest rate from this point, reaching and plateauing at 0.5 by year 25. All rotational strategies led to a small decrease and then increase in average heterosis from years 8-20. From year 20, average heterosis under UTR decreased again, down to a minimum of 0.53, whereas average heterosis under both TR and DTR increased and plateaued, reaching a maximum of 0.75 by year 33.

Figure 6.5. Annual average heterosis in cows, from years 0-40 under the previously tested true rotation strategy, the two new specific sire strategies, the composite strategy and the strategy where F1 replacements are bought in annually.

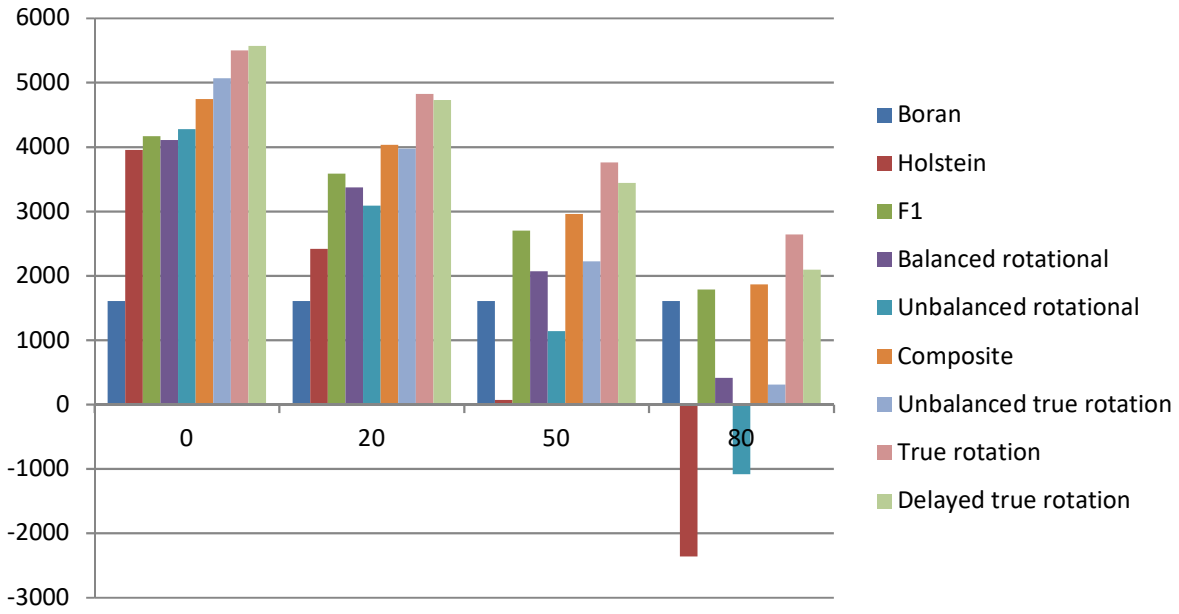


The buying F1s strategy led to constant average heterosis and Holstein genes of 1 and 50% respectively, as across all years, all cows are F1s which express maximum heterosis and have 50% Holstein ancestry.

6.3.2 Varying Survival

Without modelling any additive genetic variation in cow death rates (Y_{Death} = 0), all strategies tested led to large increases in average annual profits compared to those of the initial herd of Boran. However under scenarios where Holstein death rates are increased, the difference between these profits decreases (Figure 6.6). These decreases vary in magnitude for differing strategies so that the ranking of strategies also changes under varying genetic effects on survival.

Figure 6.6. Average annual profit per cow from years 0-40 for each strategy whilst varying negative Holstein breed additive effect for survival rate from 0 to 80% of the Boran.



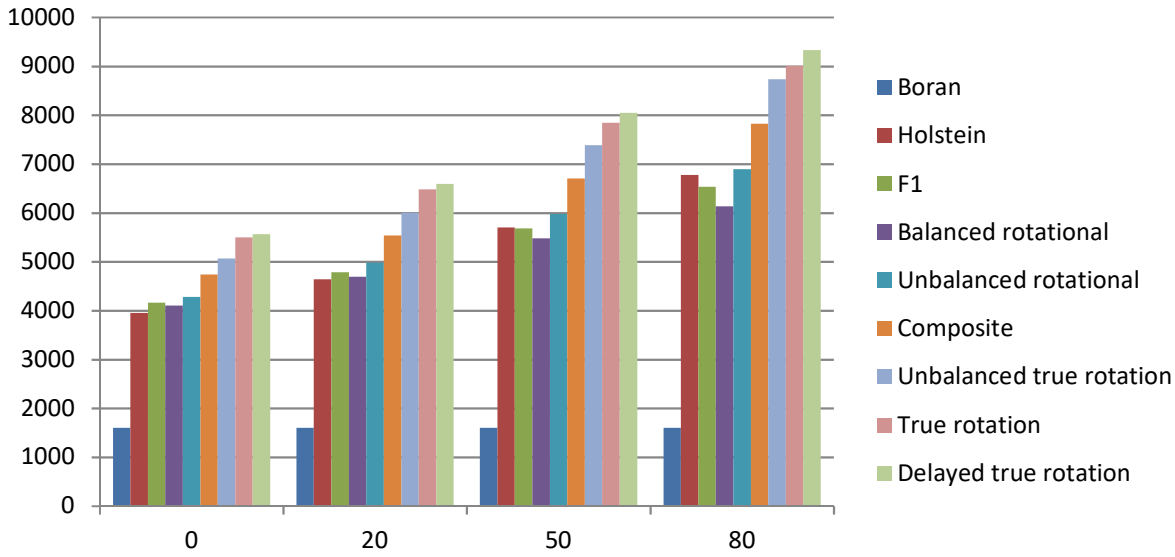
Under a scenario where Holstein death rates are 20% higher than Boran, TR and DTR continued to lead to the highest average annual profits of any strategies tested (Figure 6.6). The profits of the Holstein, unbalanced rotational and UTR strategies were reduced more than profits under other strategies tested, resulting in the F1 sire and composite strategies performing somewhat better than when no variation in death rate was modelled.

Under a scenario where Holstein death rates are 50% higher than Boran, average annual profits under the Holstein sire and unbalanced rotational strategies were lower than annual profit of the initial Boran herd (Figure 6.6). TR and DTR continued to lead to the highest profits, although TR outperformed DTR by a greater amount compared to the 20% scenario.

Under a scenario where Holstein death rates were 80% higher than Boran, four of our strategies (Holstein sire, balanced rotational, unbalanced rotational and UTR) led to lower average annual profits than those of the initial herd of purebred Borans (Figure 6.6). The F1 sire, composite and DTR strategies led to similar but slightly higher profits compared to those of the purebred Boran herd. TR led to larger average annual profits and the amount by which it outperformed all other strategies was much greater under this scenario than the others tested.

Modelling increasing negative heterosis effect for death rate led to increased average annual profits for all strategies tested and fewer changes in ranking of strategies compared to the scenarios where the additive effects for survival were varied (Figure 6.7). DTR remained the best for maximising average annual profits, whether heterosis was 0-80% of the Boran, whereas the increases in profits under increasing heterosis were comparatively smaller for the F1 and balanced rotation.

Figure 6.7. Average annual profit per cow from years 0-40 for each strategy whilst varying positive heterosis effect for survival rate from 0 to 80% of the Boran.



We found that when the Holstein death rate was at least 30.5% greater than the Boran, the Holstein sire strategy led to lower average annual profit from years 0-40 (1603 Birr per cow) than the annual profit of the initial herd of Boran (1604 Birr per cow). This threshold increased to 41.2%, 59.4% and 81.5% when death rate heterosis was -20, -50 and -80% of the Boran respectively. The initial Boran had greater average annual profit than any crossbreeding strategy when death rate heterosis was 0 and the Holstein death rate was 106.3% greater than the Boran.

6.4 Discussion

6.4.1 New strategies

The aim of the first two new strategies was to build on TR, which performed well in terms of profit and EI, and see if it could be improved. If we consider an average from years 0-40, DTR achieved this, leading to a higher average annual profit per cow than TR (5567 Birr rather than 5499 Birr) and a slightly lower milk EI (2.02 rather than 2.03 kg CO_2 eq. per kg FPCM),

whereas, despite following a similar pattern initially, UTR did not lead to a higher average profit over the period modelled (5069 Birr per cow per year from years 0-40) or a lower milk EI (2.11 kg CO_2 eq. per kg FPCM).

Initially, both DTR and UTR led to less time to reach 50% Holstein genes, meaning milk yields increased more quickly. However the production of 75% Holstein individuals under these strategies from year 5 was undesirable in terms of both profit and EI because it led to increased feed costs and reduced reproductive performance of the herd. This agrees with a review of crossbreeding cattle in the tropics which found 75% exotics were not favoured due to small increases in milk yields but large reductions in fertility (Mcdowell, 1985). In years 5-11, the presence of these individuals under both DTR and UTR explains the lower annual profits relative to TR. However, after this period, annual profits under both DTR and UTR increased to above those of TR due to the small reduction of Holstein genes in the herd. From year 17, decreases in heterosis and increases in Holstein genes under UTR led to lower annual profits compared to DTR. DTR maintained a high annual profit for this period, the same as the maximum achieved by TR by maintaining a high level of heterosis. As discussed in the previous chapter, this high level of heterosis is beneficial for profitability as heterosis for traits affecting income, particularly milk yield, is much greater than for traits affecting costs, particularly live weight which is used to predict feed costs. Therefore strategies which increase heterosis increase income to a greater extent than costs, increasing profits.

The composite strategy was designed as an alternative strategy which reduced the need for AI by reducing the frequency of use of Holstein sires. Predicted annual profits under this strategy are very similar to those of the F1 sire strategy and both use the same sire types for all but the first generation of crossing. Because the composite strategy uses a Holstein rather than F1 sire in the first generation, the proportion of Holstein genes increases from 0 to 50%

more quickly than under the F1 sire strategy, which explains the faster rise in annual profits. However, as with the F1 sire strategy, although this strategy maintains a desirable intermediate level of Holstein genes, it also results in lower heterosis and increased recombination after year 8, leading to reduced annual profits and slightly increased milk EI. An additional potential benefit of the composite strategy is that it would facilitate selection of sires within the local system (Kebede et al., 2018), meaning that any genotype by environment interactions are accounted for. Selection within composite sires could lead to further increases in herd profitability and EIs. However it would require much larger systematic data collection across larger groups of farms, both for pedigree and phenotypic records.

The buying F1s strategy led to constant annual profits and emissions due to a constant herd composition. This led to much higher annual profits than any of the breeding strategies in years 0-4 because the change in herd composition under the breeding strategies occurred more slowly. However on average from years 0-40, this strategy led to lower annual profit due to the additional costs of buying in replacements. Despite the high annual herd GHG emissions from this strategy due to the increased size of F1s, it did lead to the lowest estimated milk EI of any strategy tested, due to the high milk yield of F1s. However as we only consider GHG emissions from within the herd, the emissions from the production of bought-in replacements, which occur off farm, are not included in our calculations. Therefore, the true milk EI under this strategy will be more in line with other strategies, or potentially higher if replacements require transportation to the farm.

Another potential problem of this strategy is that it requires a good supply of F1 calves from another location. Stratified breeding systems occur in other livestock areas, for example, in the stratified sheep system in the UK, where farms can broadly be grouped into either hill,

upland or lowland. On upland farms, some ewes are crossed to lowland or terminal sires to produce lambs for use on lowland farms (Simm, 2000). There is potential to use a similar system in Ethiopia as pastoralists tend to keep purebred local animals (Rege and Tawah, 1999) as the conditions are not well suited to animals with any exotic ancestry, similar to the hill sheep farmers in the UK. These pastoralists could achieve additional income by choosing to breed some of their cows to an exotic sire, with the intention to sell all F1 calves to dairy farmers. Though this may require additional interventions to F1 calf survival as they would require additional inputs compared to purebred local calves.

6.4.2 Varying survival

As all strategies increase the proportion of Holstein genes compared to the initial herd, increasing the size of a negative Holstein effect for survival reduces annual profits for all strategies by increasing the number of replacement heifers required to be kept or bought in to maintain the herd size. However the magnitude of this reduction in profits varies between strategies and therefore their ranking for maximising profits changes across scenarios tested. Strategies which result in a high proportion of Holstein genes, particularly the Holstein sire, unbalanced rotation and UTR are most strongly affected. These strategies lead to the production of more high proportion Holstein individuals, who are more likely to die, meaning more replacements must be kept or bought in to maintain the herd, increasing costs and decreasing profits. TR and DTR are less affected by the variation of Holstein survival, maintaining increases in average annual profit, even at an 80% increase in Holstein death rate, partly because of large increases in income achieved by these strategies, but also because they have a lower proportion of Holstein genes in the herd, so survival rates and replacement costs are not as strongly affected.

Introducing a negative heterosis effect for death rate increased profits under all strategies, as all strategies led to some increases in heterosis. Under scenarios with a negative heterosis effect, this led to fewer deaths of cows and therefore less cost associated with rearing replacement heifers to maintain a constant herd size. However varying the heterosis effect led to fewer changes in strategy rankings compared to varying the additive breed effect. This is due to heterosis already being the main driver for predicting profitability and therefore the ranking of strategies, with those with high heterosis tending to be the best for maximising profits. Introducing a negative heterosis effect for death rate increases the superiority of these strategies and therefore does not have much effect on the ranking.

Although these scenarios consider variation in survival, it is important to consider that these increased environmental pressures may also affect exotic performance for many of the other traits modelled, in particular milk yields, fertility traits and veterinary costs, which will in turn affect profitability and emissions. In, for example, a scenario where the presence of a disease reduces Holstein survival, it would also likely reduce milk yield and fertility and increase veterinary costs, further reducing the potential profits of any breeding strategy which uses Holsteins.

6.4.3 Conclusion

The profitability and milk EI results for the new strategies tested highlight the importance of using a strategy that maximises heterosis. Although we have shown that for this system the buying F1 strategy, which takes this idea to the extreme, is not realistic due to the additional costs. These strategies which maximise heterosis continued to perform well even under variation in survival. However our results do highlight the need for more data on the presence of genetic variation for survival in order to more accurately predict the results of

crossbreeding strategies. In particular, it is important to identify scenarios where survival of exotics is so poor that any crossbreeding would, in fact, reduce profit. In these cases, farmers could choose to maintain a herd of the local breed or consider other interventions to reduce the mortality of crossbreds.

Chapter 7: General Discussion

7.1 Introduction and thesis objectives

Cattle are important in supporting development in SSA as they are a source of both food and income (Wood et al., 2006). However studies show there is a substantial gap between the potential and realised production levels for livestock farming in this region due to shortfalls in management but also choice of appropriate animal genotypes (Henderson et al., 2016). This gap leads to potential profit and efficiency levels not being reached. In particular, herds that have poor efficiency also tend to produce more GHGs per unit of food product. The lack of consistent recording systems for both pedigree and performance data makes selective breeding difficult. Crossbreeding strategies require comparatively little data, are generally easy strategies to follow and results can be achieved more quickly (Simm, 2000), so are a good fit in SSA systems. Crossbreeding also allows farmers to take advantage of the complementary fitness traits from local breeds and production traits from exotics, as well as providing favourable heterosis (Cunningham and Syrstad, 1987). In order to determine an optimal crossbreeding strategy, models which predict the long-term outcomes of varying strategies are needed.

Therefore, this thesis aimed to assess the potential for crossbreeding strategies to increase productivity and profitability and decrease GHG emissions and emission intensity of cattle farming in SSA. To achieve this, the main objectives were:

1. To gain a greater understanding of the expression of additive and non-additive genetic effects in crossbred cattle in the tropics.
2. To predict the performance of crossbreds not only for production, but also for other important traits.

3. To predict the long-term effects of crossbreeding strategies on herd composition.
4. To predict how this varying herd composition affects productivity, profitability and GHG emissions.
5. To use these models to assess a range of crossing strategies for a specific exemplar case study system and consider how changes to that system may affect which strategy is optimal.

7.2 Thesis Overview

In order to address the first objective, in chapter 2 a meta-analysis of heterosis in cattle in the tropics, exploring the effects of trait, breed pairing and environment, was conducted. Results showed that the majority (89.8%) of instances of significant heterosis were beneficial for the trait being studied. Traits that have an important impact on the efficiency of a farm, such as fertility, health and longevity were found to show moderate to high beneficial heterosis, suggesting that a well-designed crossbreeding strategy could lead to more efficient systems. In addition, the large beneficial heterosis seen for milk production traits is particularly promising because increasing milk production will directly increase productivity and income for farmers. The greatest heterosis was seen between breeds that are adapted for different environments, suggesting that crossbreeding strategies that use a local tropical breed and an exotic temperate breed are likely to be successful.

With results from chapter 2 confirming the potential benefits of strategies where local cattle are crossed to exotics, models were developed which could be used to compare strategies of this type. Firstly, in order to model how a strategy changes the composition of a herd over time (objective 3), we needed to predict calving rates of different crossbred animals at

different ages. Results of chapter 2 highlighted the lack of relevant fertility parameters needed for this. Therefore, in chapter 3, three models were developed which use age at first calving and calving interval to predict age-specific calving rates, thereby also addressing the second objective of the thesis to model not just production, but other important traits. These models were tested using inputs from Ethiopia against a simulation and using inputs from UK dairy cattle against results from a simulation as well as real values. The model that performed best was one which reduced estimation errors by reducing the size of age classes considered. As the increased computation needed for this model was not large, it was used to predict calving rates for potential crossbreds within our case study of Boran x Holstein crossbreeding in Ethiopia.

Chapter 4 addressed the third objective, developing a model to predict herd composition under varying strategies, using input parameters from crossbreeding studies in the meta-analysis in chapter 2 and fertility parameters predicted from our model in chapter 3. This model was used to assess the performance of a range of strategies for a case study of Boran x Holstein cattle in Ethiopia. Results for herd composition were combined with predicted performance for milk yield and yearling weight of crossbred individuals from Dickerson's crossbreeding model (Dickerson, 1973), described in chapter 1. For milk yield, strategies which increased the proportion of Holstein genetics whilst maximising heterosis and reducing recombination, tended to perform best. For yearling weight, all strategies increased the herd performance of this trait compared to the initial herd of purebred Borans, which is undesirable as heavier yearlings have greater feed costs. Strategies that minimized the proportion of Holstein genetics, such as using a crossbred sire, tended to perform best. These results also address the first part of the fourth objective of the thesis, predicting annual milk yield for varying crossbreeding strategies, finding that a strategy

which rotates between Boran and Holstein sires every generation maximised herd productivity within the Ethiopian system modelled.

In order to address the rest of the fourth objective to predict herd profitability and GHG emissions under varying crossing strategies, further development of the model was needed, from one that predicted herd performance for individual traits, into one that combined results for multiple traits into annual profit and GHG emissions predictions. This was achieved in chapter 5 which describes our economic and GHG models, developed using the Intergovernmental Panel on Climate Change Tier II framework. The model was again used to test a range of crossbreeding strategies for a case study of Boran x Holstein cattle in an Ethiopia system. Of strategies tested, results showed that a strategy where an F1 sire was used every year led to the lowest annual GHGs per animal, because the use of a crossbred sire led to smaller increases in the proportion of Holstein genes and high recombination loss expression in the herd, which led to smaller animals which produced less methane and NO_2. However, the strategy where sire type was alternated every generation (true rotational strategy) maximised annual profits and minimised the emission intensity of milk production, as it led to intermediate levels of Holstein genes which did not increase costs as much as the Holstein sire strategy and maximised heterosis which led to high milk yields and so a higher income. It also led to the lowest emission intensity for milk production due to the large increases in milk production (as shown in chapter 4) with only moderate increases in greenhouse gas emissions. This suggests that this strategy is best in the Ethiopian or similar systems for both increasing annual profits whilst also decreasing emission intensity of milk production.

The fifth objective of the thesis is addressed by results of chapters 4 and 5, where results showed that for our case study of Boran-Holstein crossbreeding in an Ethiopian dairy

system, a true rotation strategy maximised milk production and profit, whilst minimising milk emissions intensity. In chapter 6, these results were used to try to refine this strategy and test some new strategies for the Ethiopian case study. Two new rotational strategies which take advantage of the benefits of heterosis were described and tested, one with two generations of grading up to Holstein before rotating sire each generation (delayed true rotation) and another where a Holstein sire is used for two generations, a Boran sire for a single generation and this pattern continued (unbalanced true rotation). The delayed true rotation strategy led to slightly higher average annual profit and lower milk emission intensity compared to the true rotation strategy, due to the slightly higher proportion of Holstein genes. Despite the high predicted profits from rotational strategies, the implementation of these is less practical as it requires frequent use of artificial insemination. Therefore, a composite strategy was tested, which requires less artificial insemination, as most generations are sired by an F1. This strategy led to increases in annual profits and decreases in emission intensities compared to the initial herd, although less than under the rotational strategies. However, the ease of implementation may still make it an attractive alternative for farmers. Because F1 individuals tended to lead to high profits and low emission intensities, a final strategy was developed with a herd of all F1 individuals where replacement F1 heifers are bought in. Although this strategy performed well compared to the initial herd of Boran, it did not out-perform the best breeding strategies due to the additional costs of buying replacements. Overall, these results continue to highlight the importance of heterosis in determining the performance of varying crossing strategies. However, they also show that other strategies which may be easier to implement, would also lead to significant improvements in profit and emission intensities.

Finally, all strategies were tested under scenarios with varying additive and non-additive genetic variation for survival. A variety of scenarios were tested with additive genetic variation where cows with more Holstein genes were more likely to die. This reduced the profitability of all breeding strategies. In a scenario with a 50% increase in Holstein mortality compared to Boran, strategies that led to high proportions of Holstein genes led to less average annual profit than that of the initial herd of purebred Boran. A variety of scenarios where a significant negative heterosis effect for mortality was present were then tested, resulting in crossbreds tending to survive longer than when no heterosis was modelled for this trait. This resulted in increased profits under all strategies as they all lead to some heterosis, reducing the number of cows that died in a year and therefore reducing the number needed and associated costs of replacement heifers. These results show the importance of considering genetic effects for survival when designing crossing strategies and highlight the need for collection of more data on this trait.

The following sections discuss results, within context of other work, along with thoughts on further work.

7.3 Optimal strategy for Ethiopian case study

Results of chapter 5 showed all crossbreeding strategies led to increases in GHG emissions per animal compared to the initial herd of purebred Boran. As milk demand is predicted to increase (FAO, 2017a), although a no-change strategy would result in low emissions per animal, the number of animals needed to reach this demand would have to increase, resulting in in an overall increase in emissions (Hasegawa et al., 2018). To minimise

emissions whilst increasing productivity, strategies should be selected according to emission intensity rather than emissions per animal (Quinton et al., 2018).

Results from chapters 4 and 5 show that the true rotation strategy, where the sire type was alternated between Boran and Holstein every generation, resulted in the lowest milk emission intensity, as well as the highest annual milk production and profit of the five strategies tested. This is because this strategy maximises heterosis by alternating sire type and minimizes recombination loss by only using purebred sires. It also results in an intermediate proportion of Holstein genes, which balances the benefits of both breeds, the adaptability of the Boran and the higher production of the Holstein. The benefits of rotational breeding strategies to take advantage of breed complementarity and heterosis have been well described (Cunningham and Syrstad, 1987) and results presented in this thesis highlight their huge benefits for systems similar to the case study. In chapter 6, results from chapters 4 and 5 were used to try to refine the true rotational strategy, producing one strategy, the delayed true rotation where two initial generations of a Holstein sire led to quicker increases in productivity and then subsequent generations of rotation maintained high levels of heterosis. This strategy slightly outperformed the true rotational strategy in terms of profitability and milk emissions intensity in the Ethiopian case study, although the slight added complexity of the strategy may make it unattractive for such a small benefit in profit and efficiency.

Results presented in this thesis also highlight the potential problems with grading up strategies. Of all strategies tested for the Ethiopian case study, the Holstein sire strategy performed the worst for both profitability and GHG emissions, having the lowest average annual profit per cow and the highest average annual GHG emissions per cow. This is because it results in the majority of the herd having a very high proportion of Holstein genes.

These animals do not produce much more milk and therefore higher milk sales income than individuals with intermediate levels of Holstein genes, and they weigh more, which leads to higher feed costs. The strategy also performs poorly when considering GHG emissions, again due to the heavier animals produced due to the high proportion of Holstein genes. These results highlight the importance of considering long-term responses to crossing strategies. Whilst herd performance and profitability under the Holstein sire strategy were high in the first few years due to the production of many F1s, the drop in performance predicted after this led to the low average annual profits when considering a longer time period. Grading up strategies are commonly implemented across the tropics and although they perform well in the first generation, performance of subsequent generations is highly variable between systems (Cunningham and Syrstad, 1987; Galukande et al., 2013).

7.4 Implementation

When deciding on an optimal strategy, we need to consider not just the predicted productivity, profitability and GHG emissions from our model, but also the practicalities of implementation of the strategy.

Firstly, the local infrastructure may limit the potential of some strategies. In particular, the availability of artificial insemination (AI) would have a large impact as exotic sires are unlikely to be used via natural service. AI is increasingly available in parts of SSA (Guadu and Abebaw, 2016) but success rates are low (Juneyid et al., 2017) and therefore without improving the availability and success of AI, strategies that use exotic bulls will be less successful than predicted by models presented in this thesis. Therefore, the F1 sire or composite strategies

which use F1 sires may become more attractive, as they would still lead to significant increases in production, profit and efficiency compared to a herd of the local purebreds.

Secondly, the lack of pedigree recording, accurate mating records and parentage determination across many areas of SSA (Chagunda et al., 2015a) will limit the feasibility of strategies where sire type is dependent on the ancestry of the cow. For example, to implement the true rotation strategy, a farmer would need to know the sire of each cow in order to alternate sire type each generation. The superiority of this and similar strategies in terms of productivity, profit and emissions intensity suggest that efforts to overcome challenges with recording should be a high development priority, by implementing rigorous animal identification and mating schemes, using tagging of animals (Gwaza and Gambo, 2017) or genomic testing to determine breed composition (Marshall et al., 2019).

Without accurate records, strategies which use the same sire type over all cows within a year may be more practical. In particular, the unbalanced rotational strategy results in the high average annual profit whilst not requiring pedigree information for any cows and therefore is an attractive alternative.

One aspect that may require consideration for implementation is what constitutes a “herd”. In medium and large scale farms, the models could be used for a single herd. However across SSA, the majority of farms are smallholdings (Hemme and Otte, 2012). Smallholder farmers tend to keep 2-3 cows and therefore rounding errors would make these models difficult to apply, with only a subset of the genotype x age group combinations present at any one time, results could differ quite markedly from those modelled. In these situations, a group of farms, for example a single village or community, could work collaboratively to apply the models and find the optimal breeding strategy for their group of farms, similar to

community breeding projects described in chapter 1, such as goat crossbreeding programmes in Kenya (Ojango et al., 2011).

For policy makers, the results of this thesis could help to identify areas which would benefit from development. For example, results from our Ethiopian case study suggest that strategies where some of the ancestry of a cow is known tend to result in the highest profits and lowest emission intensities. Therefore the implementation of animal identification schemes, such as ear tagging, would be hugely beneficial (Gwaza and Gambo, 2017). Results from the Ethiopian case study also showed that breeding strategies that used purebred exotic sires for some generations performed well. These strategies would require the use of AI, but the infrastructure that would allow this is not in place in many areas of SSA (Guadu and Abebaw, 2016). This would therefore be a good area for development and has indeed been identified as such by other studies (Sime et al., 2014; Mwanga et al., 2019).

7.5 Limitation and difficulties

A limitation of these models is their need for genetic parameters from long-term crossbreeding studies which are representative of the system of interest. The heterogeneity of systems across SSA means that these are not available for many systems. The choice of the Ethiopian case study, although motivated in part by the desire to increase cattle farming productivity in the region (Shapiro et al., 2015), was also due to the comprehensive long-term crossbreeding study in the region (Haile et al., 2008, 2009a; b, 2011). To achieve good predictions of the results of crossbreeding strategies in other systems and with other breeds, similar long-term studies would need to be conducted.

Despite reporting genetic parameters for many important traits, the Ethiopian study does not report additive and non-additive parameters for a survival trait. Survival is highly likely to vary across different crossbreds as those with more genes from sires of temperate origin are less well adapted to SSA systems (Menjo et al., 2009). Results of the meta-analysis in chapter 1 for longevity traits suggest a significant beneficial heterosis effect for survival would be expected. Results of chapter 6 where a sensitivity analysis was carried out, varying additive and heterosis effects for death rate, show that survival rates have an important impact as they determine the number of replacement heifers needed to be reared and therefore impact both the economic and GHG costs. Survival is difficult to measure as it requires long-term monitoring of individuals which is difficult when animals are leaving the herd for a variety of reasons (Kerslake et al., 2017). For example, it may be that a cow was sold because she was performing poorly and therefore her removal could be considered selective culling, or because she was performing particularly well and therefore, she was sold for a good price to increase income. In future crossbreeding studies, recording the motivation behind an animal leaving the herd, including death and sale due to poor or high performance, would allow the estimation of genetic parameters for survival traits and would therefore allow models to provide better predictions of the outcomes of varying crossing strategies.

7.6 Further work

Expansions to the models would allow assessment of the consequences of other breeding strategies. For example, the models do not consider any variation in genetic parameters over time. If selective breeding were to be carried out in sires, the additive breed effects would be expected to improve over time, increasing herd performance over time. Selective

breeding is likely to be occurring in exotic sires, but within a temperate context, not accounting for varying selection criteria for SSA and any genotype by environment interactions. Some studies have investigated the potential of implementing sire selection for exotic breeds within SSA (Brown et al., 2016; Opoola et al., 2019) but this would rely on both the collection of more data and the development of a selection index relevant to these systems. Additionally, selective breeding could occur within the local breed and some projects have attempted this, but with inconsistent results, due to inconsistencies in selection criteria (Chawala et al., 2017). Selective breeding could also occur within crossbred populations. This would be particularly important in improving the performance of a composite strategy, which would facilitate selection of sires within the local system (Kebede et al., 2018), meaning that any genotype by environment interactions are accounted for. Selection of composite sires could lead to further increases in herd profitability and reductions in EIs. However, it would require much larger systematic data collection across larger groups of farms, for both phenotypic and pedigree or genomic records.

Also, the models presented in this thesis use the IPCC tier II approach to estimate GHG emissions as data required tended to be available for the Ethiopian system. However a life cycle assessment (LCA) approach (MacLeod et al., 2018; Salmon et al., 2018) would capture the effect of strategy on all the emissions associated with the system, including emissions associated with the production of cattle feed. As variation in emissions in our models is primarily driven by feed requirements, an LCA approach is unlikely to change the ranking of strategies in terms of GHG emissions. However, it may increase the margins between strategies.

7.7 Conclusion

Results of this thesis demonstrate the huge potential for crossbreeding to be used to increase the productivity and profitability and reduce GHG emissions for cattle herds in SSA. Models developed allowed crossing strategies to be tested and refined and an optimal strategy developed for a specific system. However, findings also highlight the need for more data collection to facilitate the modelling of other systems in SSA.

We recommend that for farms where the implementation of selective breeding programmes is unrealistic, crossbreeding should be used to increase productivity and profitability, as well and reducing emissions intensity. In order to assess which crossbreeding strategy is optimal for a farm, models developed in this thesis should be used, along with system-specific inputs. In particular, results for the Ethiopian case study suggest that rotational strategies, which maximise heterosis, should be considered. However, the practicalities of strategy implementation will also need to be considered and results for the Ethiopian case study show that even strategies which do not perform optimally, are likely to lead to significant increases in productivity, profitability and efficiency.

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